CONTRASTING SURVIVAL STRATEGIES OF HATCHERY AND WILD RED DRUM: IMPLICATIONS FOR STOCK ENHANCEMENT

A Dissertation

by

JESSICA LOUISE BECK

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

May 2008

Major Subject: Wildlife and Fisheries Sciences

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Approved by:

Chair of Committee,	Jay R. Rooker
Committee Members,	Christopher D. Marshall
	Kirk O. Winemiller
	James L. Pinckney
	Gregory W. Stunz
Head of Department,	Thomas E. Lacher

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ABSTRACT

Contrasting Survival Strategies of Hatchery and Wild Red Drum:
Implications for Stock Enhancement. (May 2008)
Jessica Louise Beck, B.S., Indiana University of Pennsylvania;
M.S., Florida Institute of Technology
Chair of Advisory Committee: Dr. Jay R. Rooker

Post-release survival of hatchery fishes is imperative to the success of any supplemental stocking program. The purpose of this research was to identify differences between hatchery and wild red drum (*Sciaenops ocellatus*) and determine if pre-release exposure techniques improve survival of hatchery individuals. Objectives were to contrast survival skills of hatchery and wild red drum from different locations, and examine if exposure to natural stimuli (e.g., habitat, predators, live prey) enhances survival skills in naïve hatchery red drum. Laboratory trials using high-speed videography (250 frames per second, fps) and field mesocosm experiments were used to investigate differences in prey-capture (e.g., attack distance, mean attack velocity, capture time, maximum gape, time to maximum gape, gape cycle duration, and foraging behaviors) and anti-predator performance (e.g., reaction distance, response distance, maximum velocity, time to maximum velocity, mean acceleration, and maximum acceleration) of hatchery and wild red drum.

Results indicated that anti-predator performance measures differed significantly between hatchery and wild red drum. Variability in prey-capture and anti-predator performance for hatchery and wild red drum was high (CV range: 5.6 – 76.5%), and was greatest for hatchery fish for the majority of performance variables tested. Exposure to habitat (*Spartina alterniflora* marsh) did not appear to afford any obvious survival benefits to hatchery red drum, although survival skills did vary according to ontogenetic stage. Hatchery red drum exposed to natural predators (pinfish, *Lagodon rhomboides*) exhibited significantly greater attack distances during feeding events, and anti-predator

performance variables were 20 – 300% in these individuals versus naïve red drum. In predation experiments with free-ranging pinfish predators, mortality rates (*Z*) ranged from 0.047 – 0.060 $h^{-1} \cdot predator^{-1}$; however no significant differences in mortality were found between fish reared with and without predators. Hatchery red drum reared on live prey (*Artemia franciscana*, mysid shrimp) demonstrated enhanced prey-capture and foraging behaviors as well as anti-predator performance relative to fish reared on artificial (pellet) diets. Findings of this research indicate that several behavioral patterns differed between hatchery and wild red drum; however, these differences can be mediated through the use of various pre-release exposure techniques.

DEDICATION

I dedicate this work to my family for all of their love and support throughout the course of my graduate career.

ACKNOWLEDGEMENTS

First and foremost I would like to extend my deepest gratitude to my advisor, Dr. Jay Rooker, for his guidance and support over the past five years. Thank you for your continued words of wisdom and for providing me with the confidence to pursue this degree, especially during the difficult times. You have truly been an incredible mentor and friend and I am extremely grateful for the opportunity to be a part of the Rooker Lab.

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CHAPTER I

INTRODUCTION

Stock enhancement involves the large-scale release of hatchery-reared progeny in order to boost natural populations of commercially and recreationally important fish species (Lorenzen 2005). This practice dates back to 1870s Norway, when cultured Atlantic cod (*Gadus morhua*) larvae were released into the ocean in an attempt to prevent the collapse of the fishery (MacCall 1989). Several decades later, the U.S. and Japan began their own supplemental stocking programs, releasing cod (*G. morhua*), herring (*Clupea harengus*) and salmon (*Salmo salar*) fry into local waters (Richards and Edwards 1986; Kitada 1999). To date, over 250 species of finfish worldwide have been the focus of similar enhancement efforts (Welcomme and Bartley 1998). Yet, the viability of hatchery release programs remains a controversial subject as few stocking programs have been shown to successfully increase overall fishery yields (Richards and Edwards 1986; Cowx 1999; Svasand et al. 2000).

The primary goal of any stocking program is to produce hatchery progeny which are identical to their wild counterparts (Brown and Laland 2001). Nevertheless, research has shown that hatchery individuals differ considerably in terms of their behavior, morphology, and physiology compared to wild fishes (Fleming et al. 1994; Ellis et al. 1997; Munro and Bell 1997; McDonald et al. 1998; Olla et al. 1998; Stunz and Minello 2001; Hill et al. 2006; Basaran et al. 2007). For example, deficiencies in the ability of hatchery fish to capture natural prey (Suboski and Templeton 1989; Wiley et al. 1993; Olla et al. 1998; Brown and Laland 2001), recognize and avoid predators (Patten 1977; Suboski and Templeton 1989; Olla et al. 1998; Brown and Warburton 1999), and use complex habitats (Brown and Laland 2001; Stunz and Minello 2001) are well documented. In many cases, these behaviors have been attributed to the 'psychosensory deprived' environment in which these fish are raised as these areas are typically void of

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This thesis follows the style of Transactions of the American Fisheries Society.

natural stimuli (Olla et al. 1998). Consequently, hatchery fish often lack basic survival skills inherent in their wild counterparts, resulting in high rates of mortality and low returns of stocked individuals.

Although the rearing experience may reduce the ability of hatchery fish to survive in the wild (Olla et al. 1994; Munro and Bell 1997), there is evidence that pre-release exposure to natural stimuli can substantially improve survival success in these individuals (Jarvi and Uglem 1993; Brown and Laland 2001). Maynard et al. (1996) showed that chinook salmon (*Oncorhynchus tshawytscha*) reared with live prey exhibited improved feeding behaviors relative to fish reared on artificial (pellet) diets. Similarly, hatchery coho salmon (*O. kisutch*) exposed to predators demonstrated an increase in escape performance relative to naïve fish (Ginetz and Larkin 1976; Olla and Davis 1989). Enrichment of rearing environments with structure or complex habitat has also been linked to the development of more naturalistic behaviors in hatchery fish, leading to higher rates of survival following release (Braithwaite and Salvanes 2005; Salvanes and Braithwaite 2005). Nevertheless, such pre-release exposure techniques are rarely used by hatchery managers due to lack of information on the proper methods and circumstances under which they should be implemented (Brown and Laland 2001).

Red drum stock enhancement in Texas

Historically, red drum (*Sciaenops ocellatus*) supported a thriving commercial and recreational fishery in the Gulf of Mexico (Scharf 2000). Severe stock declines in the 1980s resulted in the closure of the commercial fishery and the implementation of a large-scale hatchery-release program by the Texas Parks and Wildlife Department (TPWD). The goal of the program was to supplement natural recruitment of red drum and increase populations in the Gulf of Mexico by stocking juveniles (20-30 mm total length) into Texas bays and estuaries. Over twenty years later, this program represents one of the largest marine fish stocking programs in the Gulf, releasing approximately 30 million red drum fingerlings into local bays and estuaries each year (Vega et al. 2003).

While red drum numbers have steadily increased along the Texas coast since their initial decline (Pattillo et al. 1997), the contribution of TPWD juveniles to the total population remains largely unknown (Scharf 2000). Previous recapture studies that have attempted to evaluate the success of this program have been questioned as they have often produced conflicting results (McEachron et al. 1998; Scharf 2000). In addition, experimental evidence has shown that hatchery red drum experience higher mortality (Rooker et al. 1998; Stunz and Minello 2001) and exhibit deficiencies in their behavioral performance (e.g., survival skills) relative to wild individuals (Smith and Fuiman 2004). As with other reared species, there is concern that the lack of natural stimuli (e.g., habitat, predators, live prey) in the rearing environment may depress the development of critical survival skills in red drum, resulting in poor survival success of stocked individuals. Unfortunately, prior to this research, there has been little information regarding the impact of early life experience(s) on the survival success of hatchery red drum.

Objectives

The overall goal of my research was to examine differences in the survival skills of hatchery and wild red drum and evaluate whether pre-release exposure to natural stimuli could be used to enhance hatchery red drum survival in the wild. The primary objectives of my dissertation were as follows:

1. Compare and contrast survival skills (e.g., prey-capture and anti-predator performance) of hatchery and wild red drum from several hatcheries and bays, respectively.
2. Determine the impact of exposure to natural habitat (*Spartina alterniflora* marsh) on the survival skills of hatchery red drum.
3. Determine the impact of exposure to natural predators (pinfish, *Lagodon rhomboides*) on the survival skills and mortality rate (*Z*) of hatchery red drum.
4. Determine the impact of diet (pellet versus live prey, *Artemia franciscana* and mysid shrimp) on the survival skills and foraging behaviors of hatchery red drum.

CHAPTER II

PREY-CAPTURE AND ANTI-PREDATOR PERFORMANCE OF HATCHERY AND WILD RED DRUM: ARE SURVIVAL SKILLS IMPACTED BY EARLY LIFE EXPOSURE?

Introduction

The use of stock enhancement as a fisheries management tool is a controversial subject (MacCall 1989; Bowles 1995; Grimes 1998). For over a century, large-scale hatchery releases have been conducted in an attempt to boost declining populations of marine fishes (Moring 1986), yet few of these efforts have led to an increase in overall fishery yields (Richards and Edwards 1986; Hilborn and Winton 1993; Cowx 1999; Svasand et al. 2000). Poor survivorship of hatchery progeny has been attributed to the failure of many stocking programs, as hatchery individuals appear to lack basic survival skills inherent in their wild counterparts. For example, hatchery fish have been shown to demonstrate deficiencies in their ability to capture prey (Wiley et al. 1993; Brown and Laland 2001), and avoid predators (Patten 1977; Brown and Warburton 1999; Stunz and Minello 2001). Early life exposure to the 'psychosensory deprived' hatchery environment has been associated with these deficits, as these areas are typically void of many or all natural stimuli (e.g., prey types, predators, habitat) (Olla et al. 1998).

The red drum, *Sciaenops ocellatus*, is a highly prized sportfish which is the focus of several large-scale stock enhancement programs along the U.S. Atlantic and Gulf coasts (Smith et al. 2001). In some states, red drum stocking efforts have been associated with the recovery of natural populations (McEachron et al. 1995, 1998; Jenkins et al. 2004); however, experimental evidence suggests that hatchery red drum may lack certain survival skills compared to their wild counterparts (Smith and Fuiman 2004). It is possible that such behavioral discrepancies may result in increased mortality in hatchery red drum following release (Rooker et al. 1998; Stunz and Minello 2001), leading to poor returns of stocked individuals.

Here, I investigated whether early life exposure impacts survival skills of red drum. This work is based on the premise that early life exposure to natural stimuli enhances prey-capture and anti-predator performance (i.e., 'survival skills') of hatchery and wild red drum. To assess the impact of early life exposure, I collected red drum from three hatcheries and three bay systems and used high-speed video to quantify a suite of variables previously linked to survival. In addition to evaluating overall differences in survival skills between hatchery and wild red drum, I examined whether these skills also differed among the three hatcheries and among the three bay systems, since there is strong evidence that different populations of the same species will vary their behavioral performance in order to meet the demands of their environment (Taylor and McPhail 1985; Nicoletto and Kodric-Brown 1999; Nelson et al. 2003). Knowledge of such intraspecific differences may allow hatchery managers to more closely match hatchery fish to wild populations, thereby increasing post-release survival of stocked progeny (Conover 1998).

Methods

Collection of hatchery and wild red drum. – Red drum juveniles (20-30 mm standard length, SL) were obtained from three hatcheries and three bay systems along the Texas coast from 3 November 2005 to 16 November 2005 (Figure 1). Hatchery red drum were sampled from two Texas Parks and Wildlife Department hatcheries (TPWD), the Coastal Conservation Association/Central Power and Light Marine Development Center (MDC), Flour Bluff, Texas, and the Perry R. Bass Marine Fisheries Research Center (PRB), Palacios, Texas. Fish reared at MDC and PRB represented separate batches of red drum spawned (six days apart) from the same broodstock at MDC (2-3 females and 2-3 males per tank, 8 tanks), which were induced to spawn using artificial temperature and photoperiod regimes. Fertilized eggs were collected and reared in 12,000-l tanks at MDC until three days post hatch (dph), when they were transferred to a 1-acre polyethylene lined pond at MDC and 2-acre earthen pond at PRB. Fish in both ponds had access to shrimp nauplii, calanoid copepods, rotifers and polychaete worms.

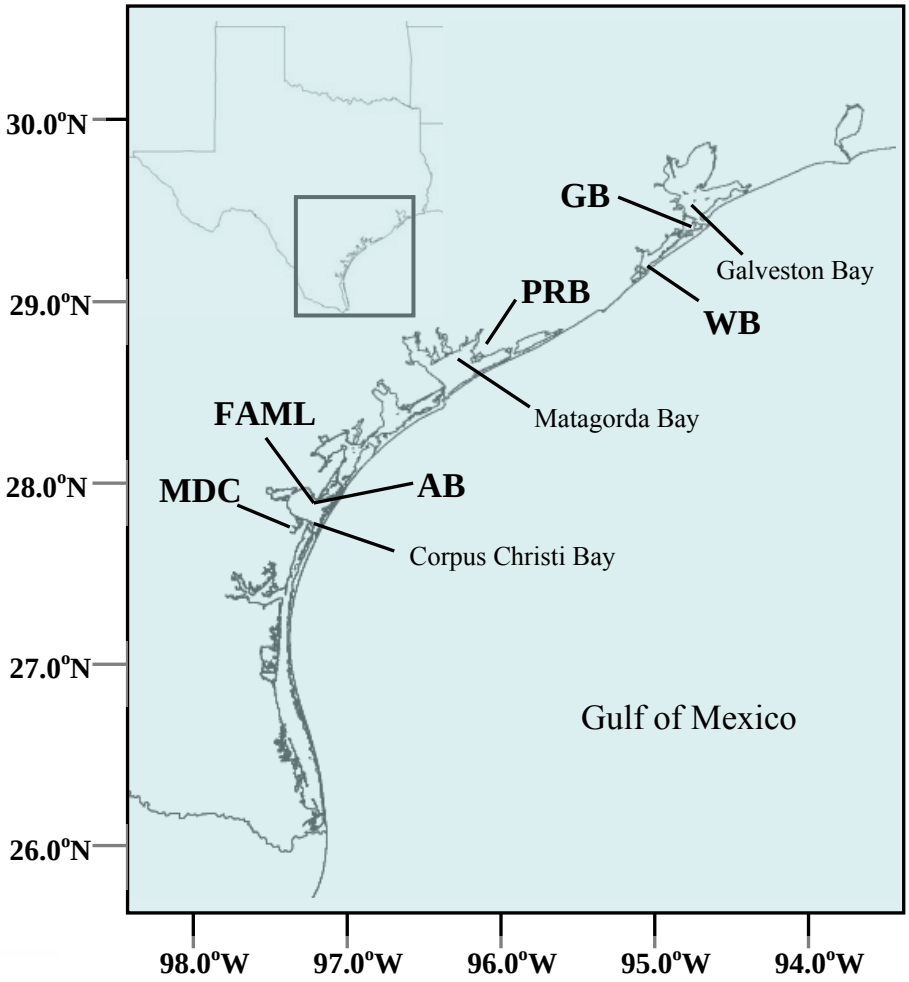

Figure 1. Map of the Texas coast showing location of red drum hatcheries and bay systems. Hatcheries: MDC = Coastal Conservation Association/Central Power and Light Marine Development Center, PRB = Perry R. Bass Marine Fisheries Research Station, FAML = Fisheries and Mariculture Laboratory. Bay systems: AB = Aransas Bay, GB = Galveston Bay, WB = West Bay.

In addition, ponds were supplemented with 2-6 lbs of high-protein commercial feed (Nelson and Sons, Inc.) up to five days a week beginning 18 days after stocking. Hatchery red drum were also collected from captive broodstock (2-3 females and 2-3 males per tank, 6 tanks) at the Fisheries and Mariculture Laboratory (FAML) at the University of Texas Marine Science Institute. These fish were reared in 400-l tanks from hatching and fed a diet of enriched rotifers (*Brachionus* spp.) from 3 to 9 days post hatch. At day 10, FAML fish were switched to a mixture of enriched *Artemia franciscana* supplemented with high-protein dry feed (Skretting's Apollo Starter). Red drum from MDC and PRB were acquired during pond harvesting, and were randomly sampled from transport trailers. Fish from FAML were sampled at random from holding tanks using a dip net.

Wild red drum were collected from three bay systems along the Texas coast: Aransas Bay (AB), Galveston Bay (GB), and West Bay (WB) (Figure 1). A 50-foot bag seine was pulled parallel to the shore at a distance of 10-15 m from the shoreline. Several areas at each location were sampled and fish were collected over shoal grass (*Halodule wrightii*) habitats in AB and WB, and over non-vegetated bottom in GB.

Experimental design and high-speed videography. – Immediately after collection, red drum were transported to a wet lab in Galveston, Texas, and held overnight in fiberglass tanks (1.5 m diameter, 0.75 m deep). All tanks were filled with sand-filtered seawater pumped from the Gulf of Mexico (26.5-29.2^{o}C, 32-33 ppt). The following morning, ten red drum from each location (n = 10) were chosen at random and placed into separate chambers (18 cm x 10 cm) in preparation for filming trials. Prey-capture and anti-predator performance was recorded for each fish at 250 frames per second (fps) using a high-speed video camera (Redlake MotionScope PCI 1000S). A 1-cm x 1-cm grid placed behind the fish was used to provide scale during all filming events. Each event was referenced to time zero, corresponding to the frame prior to mouth opening during feeding, and the frame immediately preceding the first movement of the fish during an anti-predator response.

Prey-capture performance was evaluated by filming individual fish feeding on mysid shrimp (Mysidacea spp., < 4 mm total length), a major prey item for red drum larvae and juveniles (Soto et al. 1998). Several mysid shrimp were released into the chamber at a time and feeding events were recorded until red drum became satiated. Only those feeding events that occurred laterally to the camera were used in the final analysis and four variables were recorded for each prey-capture event: (1) attack distance, distance from the tip of the premaxilla to the closest point on the prey at the beginning of prey capture (mm), (2) mean attack velocity, average red drum velocity from time zero to when prey completely entered the mouth (mm/s), (3) capture time, time to when prey completely entered the mouth (ms), and (4) gape cycle duration, time elapsed from time zero to when mouth closes (ms).

Following feeding trials, fish were moved to a separate control box to record anti-predator performance for each individual. Anti-predator performance was elicited by releasing a visual stimulus consisting of a 4.5-cm diameter bulls-eye target on a swinging pendulum arm. This stimulus was modeled after Batty (1989) and has been shown to produce anti-predator behaviors in red drum larvae and juveniles (Fuiman and Cowan 2003; Smith and Fuiman 2004). Anti-predator sequences were filmed from above and began when the fish was near the front of the container and facing less than 90º toward the direction of the stimulus. When the subject was in position, the pendulum was released, sending the target toward the subject. Four variables were recorded for each anti-predator event: (1) reaction distance, distance between red drum and center of target at time zero (mm), (2) response distance, distance traveled during the first 100 ms of response (mm), (3) mean velocity, averaged velocity over the duration of response (mm/s), and (4) maximum velocity, maximum velocity reached during response (mm/s). For all anti-predator events, only the first 100 ms were analyzed since fish often made contact with the sides of the chamber or swam out of the field of view after this time. Each fish was given 15-20 min between successive events in order to allow for recovery time and to prevent habituation to the stimulus.

On average, three prey-capture and three anti-predator events were recorded for each individual fish (3 events x 10 fish x 2 treatments). Video footages were analyzed at 2-4x magnification using Redlake MotionScope 2.30.0 and Peak Motus 8.0 software. Displacement data were generated by tracking a digitized point on the center of the eye during prey capture, and on the center of mass (~30% from tip of snout, verified from preserved specimens) during anti-predator events. A generalized cross-validatory (GCV) quintic spline algorithm was applied to the displacement data for each anti-predator event in order to produce velocity values (QuickSAND, Walker 1997). This algorithm has been shown to accurately estimate velocity at the frame rate (250 fps) and magnification (2-4x) specified in this study (Walker 1998; Bergmann and Irschick 2006).

Data analysis. – Data were tested for normality and homogeneity of variances using Kolmogorov-Smirnov and Levene's tests, respectively. Five variables (attack distance, mean attack velocity, capture time, reaction distance and maximum velocity) were Ln-transformed in order to meet the assumption of normality. To correct for size-related differences between fish, variables were regressed against the length of each individual and the size-removed residuals were used in all subsequent analyses. Differences in prey-capture and anti-predator performance among origins (hatchery or wild) and among locations nested within origins (hatchery = MDC, PRB, FAML; wild = AB, GB, WB) were tested using nested multiple analysis of variance (MANOVA). Separate nested MANOVAs were conducted for prey-capture and anti-predator performance variables. Nested univariate contrasts were also generated for each prey-capture and anti-predator variable and in cases where a significant difference was found, Tukey's HSD post hoc test was used to determine which factor levels differed. All tests were performed on fish means, which were calculated by averaging the values of up to three responses per individual.

Additionally, the amount of variability within locations and among origins was calculated for each prey-capture and anti-predator performance variable. Variability was quantified using the coefficient of variation, expressed as a percentage (CV = S.D. /

mean · 100). Within locations, the CV for each variable was calculated from the mean of the ten fish sampled from that particular location (n = 10). Among origins, i.e., hatchery or wild (wild herein referred to as 'bay'), the CV for each variable was calculated from the mean at each of the three locations nested within that origin (n = 3). Statistical tests were conducted using SYSTAT 12.0 and $\alpha = 0.05$.

Results

Prey-capture performance. – No difference in prey-capture performance was detected among locations within origins (MANOVA: Pillai's Trace, F = 1.530, df = 16, 220, $P = 0.091$). Univariate contrasts also failed to detect differences among locations within origins for all four prey-capture variables. Feeding attempts on mysid shrimp prey resulted in successful acquisition of a prey item approximately nine out of ten times for all fish and individuals followed the same sequence of prey-capture events during feeding (see Beck and Turingan 2007 for further description of red drum feeding sequence). In addition, red drum exhibited similar timing in regards to gape cycle duration, which lasted for ~25 ms in both hatchery and wild fish (Table 1). Hatchery individuals appeared to demonstrate higher mean values than wild fish for attack distance, mean attack velocity, and capture time (Table 1). The magnitude of response varied between locations for each prey-capture variable (Figure 2); however, these differences were not statistically significant.

Within the six locations, the CV range for prey-capture variables was largest for attack distance (42.3 – 70.7%), followed by mean attack velocity (17.2 – 39.2%), capture time (12.2 – 22.5%), and gape cycle duration (5.6 – 13.2%) (Table 2). Red drum from FAML demonstrated the greatest variability in attack distance (70.7%), mean attack velocity (39.2%), and gape cycle duration (13.2%), while WB fish demonstrated the highest amount of variability for capture time (22.5%) (Table 2). Among origins (hatchery or bay), CV for prey-capture variables among hatcheries ranged from 3.5 – 37.1%, yet remained ≤ 7% among bays (Table 2). Interestingly, CV for attack distance and mean attack velocity were approximately five times higher among hatcheries than

Table 1. Mean (± S.E.) of prey-capture and anti-predator performance variables for hatchery and wild red drum (n = 30).

Variable	Hatchery	Wild
Prey-capture performance:		
Attack distance (mm)	0.97 ± 0.13	0.82 ± 0.08
Mean attack velocity (mm/s)	170.00 ± 11.73	152.73 ± 6.80
Capture time (ms)	11.31 ± 0.30	10.87 ± 0.36
Gape cycle duration (ms)	25.64 ± 0.50	25.91 ± 0.49
Anti-predator performance:		
Reaction distance (mm)	46.25 ± 7.41	22.70 ± 2.40
Response distance (mm)	25.02 ± 1.44	22.74 ± 1.15
Mean velocity (mm/s)	250.16 ± 14.40	227.44 ± 11.51
Maximum velocity (mm/s)	532.99 ± 34.67	516.91 ± 28.42

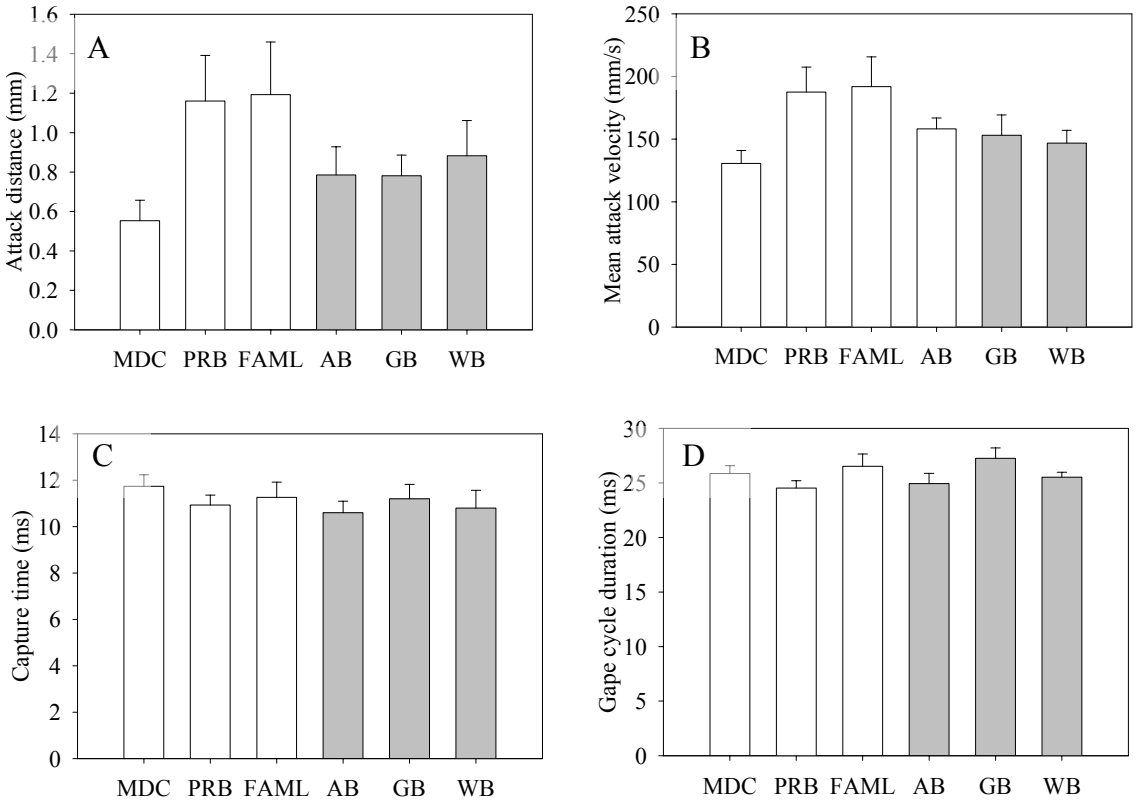

Figure 2. Mean (± S.E.) for variables associated with prey-capture performance in red drum: (A) attack distance, (B) mean attack velocity, (C) capture time, and (D) gape cycle duration. Open bars (□) designate hatchery fish, and shaded bars (■) designate wild fish.

Table 2. Variability in performance for prey-capture and anti-predator variables within each location (MDC, FAML, PRB, AB, GB, WB) and among origins (hatchery or wild) as measured by the coefficient of variation (CV = S.D. / mean · 100).

	Hatchery				Wild			
Variable	MDC	PRB	FAML	All Hatchery	AB	GB	WB	All Wild
Prey-capture performance:								
Attack distance (mm)	59.6	62.9	70.7	37.1	57.4	42.3	63.8	7.0
Mean attack velocity (mm/s)	24.9	33.6	39.2	20.1	17.2	33.5	21.7	3.7
Capture time (ms)	13.4	12.2	18.1	3.5	14.6	17.4	22.5	2.8
Gape cycle duration (ms)	8.7	8.6	13.2	3.9	11.9	10.9	5.6	4.6
Anti-predator performance:								
Reaction distance (mm)	29.7	76.5	75.0	51.4	23.9	65.7	67.2	13.0
Response distance (mm)	32.3	22.7	31.2	19.2	20.5	23.3	35.7	7.7
Mean velocity (mm/s)	32.3	22.7	31.2	19.2	20.5	23.3	35.7	7.7
Maximum velocity (mm/s)	34.8	31.9	19.8	24.6	31.7	28.9	32.5	1.9

among bays (Table 2). In contrast, CV was < 5% for capture time and gape cycle duration both among hatcheries and among bays (Table 2).

Anti-predator performance. – Red drum responded to the approach of the visual stimulus by exhibiting the characteristic C-start response (Eaton et al. 1991). Overall, a significant difference in anti-predator performance among locations within origins was detected (MANOVA: Pillai's Trace, F = 2.197, df = 16, 220, $P = 0.006$). Univariate contrasts indicated that reaction distance ($P = 0.013$), response distance ($P = 0.026$), mean velocity ($P = 0.026$), and maximum velocity ($P = 0.018$) differed significantly among locations within origins. The reaction distance of hatchery fish was approximately 2x greater than wild fish, and hatchery fish also demonstrated greater response distance and higher mean and maximum velocity compared to wild red drum (Table 1). Tukey's HSD test indicated significant differences in anti-predator performance between the six locations. Fish from FAML exhibited a greater reaction distance (70.64 ± 16.77 mm) compared to fish at all other locations, excluding PRB (45.04 ± 10.90 mm) (Figure 3A). Response distance was greater for PRB fish (30.41 ± 2.19 mm) than fish from MDC (21.13 ± 2.16 mm) and GB (20.75 ± 1.53 mm) (Figure 3B). Fish from PRB also had higher mean velocity (304.19 ± 21.92 mm/s) than fish from MDC (211.31 ± 21.60 mm/s) and GB (207.52 ± 15.35 mm/s) (Figure 3C). Lastly, PRB fish reached higher maximum velocity (676.21 ± 68.32 mm/s) during anti-predator responses compared to fish from MDC (418.59 ± 46.14 mm/s) (Figure 3D).

While there were no distinct trends within the six locations, the overall CV range was greatest for reaction distance (23.9 – 76.5%), followed by response distance (20.5 – 35.7%), mean velocity (20.5 – 35.7%), and maximum velocity (19.8 – 34.8%) (Table 2). Among origins, CV for all four anti-predator variables was greater among hatcheries than among bays, ranging from 19.2 – 51.4% and 1.9 – 13.0%, respectively (Table 2). The CV for reaction distance, response distance and mean velocity were approximately 2-4x greater among hatcheries compared to among bays, while CV for maximum

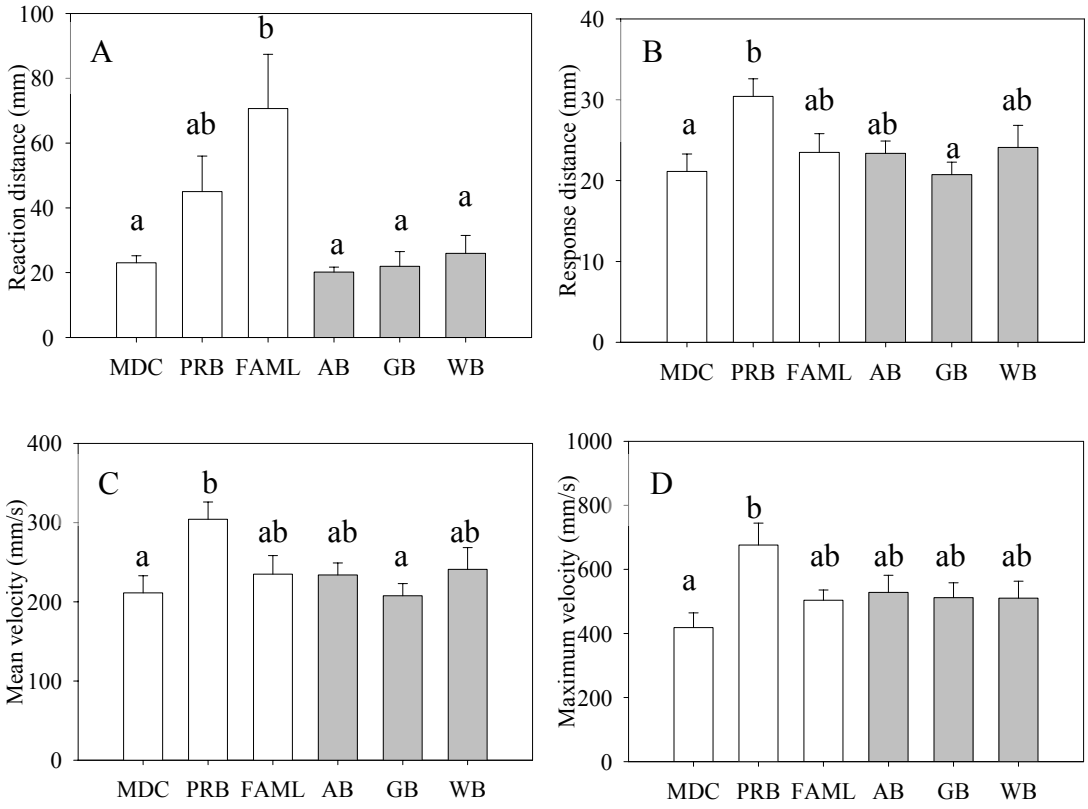

Figure 3. Mean (± S.E.) for variables associated with anti-predator performance in red drum: (A) reaction distance, (B) response distance, (C) mean velocity, and (D) maximum velocity. Open bars (□) designate hatchery fish, and shaded bars (■) designate wild fish. Lower case letters represent significant differences based on Tukey's HSD post hoc tests.

velocity was more than 12x greater among hatcheries (24.6%) than among bays (1.9%) (Table 2).

Discussion

Analysis of red drum feeding events indicated that prey-capture performance did not differ between hatchery and wild red drum. These findings conflict with previous studies which demonstrate that hatchery fish exhibit diminished feeding performance in comparison to wild individuals. In prey-capture trials, hatchery Atlantic salmon, *Salmo salar* (Sosiak et al. 1979), brown trout, *Salmo trutta* (Bachman 1984), turbot, *Scopthalmus maximus* (Ellis et al. 2002), and Florida largemouth bass, *Micropterus salmoides floridanus* (Wintzer and Motta 2005) captured fewer live prey items than their wild counterparts. Reduced feeding performance in hatchery fish relative to wild individuals may be explained by the absence of live prey in the rearing environment, as hatchery fish are typically fed commercial pellets while in captivity. However, experimental evidence has shown that exposing hatchery fish to live prey enhances their foraging ability and leads to the development of behavioral patterns comparable to those of wild fish (Paszkowski and Olla 1985; Wintzer and Motta 2005). This may explain the lack of differences in the prey-capture performance of hatchery and wild red drum in this study, as hatchery fish were exposed to live prey (e.g., rotifers, copepods, *Artemia*) throughout the rearing process.

Anti-predator performance differed significantly between hatchery and wild red drum, with greater reaction distance, greater response distance, and higher mean and maximum velocities observed for hatchery individuals (Table 1). These results are in accordance with Smith and Fuiman (2004) who found that visually-mediated startle responses were of greater distance and duration in hatchery versus wild red drum. Physical differences between the two rearing environments may have generated variability in the anti-predator performance of hatchery and wild individuals. For example, the absence of structure and enhanced water clarity within the hatcheries may have resulted in hatchery red drum being more perceptive to their surroundings, thus

leading to longer reaction distances in these fish. Alternatively, it has also been suggested that variability in the anti-predator performance between hatchery and wild red drum may stem from dietary differences (Smith and Fuiman 2004). In this study, hatchery fish diets were supplemented with high-protein (> 51%) pellet feeds. Consumption of these feeds may have provided increased energy during swimming bouts, resulting in the ability of hatchery fish to travel further and achieve higher mean and maximum velocities than wild fish. The importance of diet quality on swimming performance has been demonstrated in other species such as the Atlantic cod (*Gadus morhua*), where swimming speed was positively correlated with food availability (Björnsson 1993).

Numerous studies have demonstrated that anti-predator skills are closely linked to early life experiences. For example, Ambon damselfish, *Pomacentrus amboinensis*, with prior exposure to predators had higher survival rates following release versus predator-naïve fish (McCormick and Holmes 2006). Likewise, European minnows, *Phoxinus phoxinus*, subjected to a stalking predator model at two months old performed a greater number of 'predator inspections' when tested two years later than did minnows that had not received this exposure (Magurran 1990). In a previous study, Smith and Fuiman (2004) argued that differential experience with predators in the rearing environment may have been responsible for the increased responsiveness of hatchery red drum larvae relative to their wild counterparts. They hypothesized that wild red drum likely encountered predators prior to capture and as a result may not have perceived the stimulus as threatening, thereby leading to lower responsiveness in wild fish. Conversely, they proposed that hatchery red drum reared without predators may have been unable to discern between threatening and non-threatening stimuli, and thus reacted to the stimulus as if it were a true predator. It is likely that similar circumstances led to the increased responsiveness of hatchery red drum juveniles in this study, and this may have survival implications for these individuals. For example, anti-predator reactions are energetically expensive (Ydenberg and Dill 1986), and an increase in frequency of these reactions may reduce energy levels and overall condition of hatchery fishes

(Martínez et al. 2003), thereby placing them at higher risk for predation following release. Moreover, the time and energy spent on fleeing when no true predatory threat exists may be better spent on other important survival behaviors such as foraging (Ryer and Olla 1998).

In addition to overall differences between hatchery and wild red drum, there was significant variability in anti-predator performance among the different locations. In general, I found that anti-predator performance was highest for fish from PRB and (to a lesser extent) FAML, while lower performance measures were demonstrated for fish from AB, GB, WB and MDC. There is evidence that environmental characteristics shape the behavioral performance of fishes. For example, critical swimming velocity (U_{crit}) is positively correlated with current velocities in populations of guppies, *Poecilia reticulata* (Nicoletto and Kodric-Brown 1999) and blacknose dace, *Rhinichthys atratulus* (Nelson et al. 2003). While not directly tested, it is possible that physical differences between the six locations, e.g., prey density, salinity, habitat presence/absence, also impacted the anti-predator performance of red drum in this study. For example, fish from PRB performed consistently well for all anti-predator variables. Anecdotal evidence suggests that prey density is higher and the types of prey more diverse in PRB ponds versus MDC ponds and FAML tanks (Rodney J. Gamez, TPWD, personal communication), perhaps leading to enhanced condition in PRB fish. Additionally, stress associated with high salinity levels in the MDC ponds over the course of the study (41-45 ppt at MDC versus 25-33 ppt at the five other locations) may have contributed to the poor performance of MDC individuals during anti-predator trials. Furthermore, the absence of submerged aquatic vegetation at the GB location may have also impacted performance levels of these fish relative to fish collected from AB and WB. Experimental evidence suggests that the presence of habitat is linked to higher survival rates during the early life stages in red drum (Rooker et al. 1998; Stunz et al. 2002) and fish from GB demonstrated lower performance measures for several variables relative to AB and WB fish. These trends indicate that red drum performance may be linked to specific environmental factors, many of which may vary considerably across locations.

Variability in the prey-capture and anti-predator performance of red drum was substantial within each location. Overall, the CV range was greatest for attack distance and reaction distance, at 42.3 – 70.7% and 23.9 – 76.5%, respectively. However, the CV range was considerably lower for the remaining six variables, possibly due to the restricted size range of red drum in this study. In general, the amount of variability within locations was large relative to the inter-individual variability in critical swimming velocity (U_{crit}) reported for Atlantic salmon, *S. salar* (9.9 – 35.4%, Reidy et al. 2000) and running and swimming performance in the salamander, *Ambystoma tigrinum nebulosum* (17 – 29%, Bennett et al. 1989). Large CVs within locations for red drum may be explained by high genetic diversity of these populations since hatchery and wild individuals were both produced from multiple spawning adults. Inter-individual performance can also vary considerably based upon differences in size and condition (MacKenzie and Kiorboe 1995; Koumoundouros et al. 2002; Martínez et al. 2003). While size differences were accounted for in this model, it is possible that individual condition measures (e.g., gut fullness, RNA:DNA) varied within a population, although this was not tested directly. Interestingly, the CV within locations was comparable to the amount of intra-individual variability reported by Fuiman and Cowan (2003) for red drum larvae. This is surprising since one would expect the amount of variability within an individual to be lower than that between fish. Fuiman and Cowan (2003) attributed the high levels of intra-individual variability in their study to poor repeatability in the performance of individual larvae during test trials.

When CV was calculated among each origin (i.e., hatchery or bay), there was a higher amount of variability among hatcheries than among bays for most of the performance variables tested. Overall, the CV among hatcheries was approximately 20% or higher for six of eight variables, and this was two to five times greater than the variability among bays. Conversely, variability among bays was < 8% for all variables, excluding reaction distance (13.0%). The range of CV among bays was comparable to that reported for the U_{crit} among populations of coho salmon, *Oncorhynchus kisutch* (9.5 – 16.6%, Taylor and McPhail 1985) and yellow perch, *Perca flavescens* (9.7 – 15.6%,

Nelson 1989). While U_{crit} was comparable to the mean and maximum velocity variables in this study, I was unable to find information on the CV for the other six variables tested. It is possible that selective mortality in the wild may have substantially reduced the amount of variability among bays as these individuals were probably subjected to a range of selective pressures (e.g., starvation, predation) for several weeks prior to being captured. By contrast, abundant prey resources and absence of predators in the hatcheries likely resulted in artificially high survivorship at these locations, as has been demonstrated with Atlantic salmon, *S. salar* (50% hatchery survival versus < 1% wild survival, Piggins and Mills 1985). There is evidence that artificial conditions within hatchery environments may promote the persistence of individuals that would otherwise be unsuited for life in the wild (Weber and Fausch 2003). This is especially apparent when considering the high rates of post-release mortality experienced by hatchery fishes shortly following release (Shively et al. 1996; Brown and Laland 2001; Brown and Day 2002).

Survival of hatchery-reared fishes in the wild has been studied using mass marking techniques (Brennan et al. 2007; Cucherousset et al. 2007), or through monitoring the growth and condition of newly released individuals (Westerman and Holt 1994; Furuta 1996). However, these methods often provide little information as to the actual mechanisms driving mortality in hatchery fishes. Here, I demonstrate the value of using behavioral performance studies to gain a better understanding of the underlying factors influencing post-release mortality in hatchery individuals. Findings from the present study indicate that prey-capture performance of red drum appears to be highly developed in hatchery red drum, and this is likely a function of the use of live prey as a food source during the rearing process. By contrast, anti-predator behaviors differed significantly between hatchery and wild red drum, although greater distances and velocities exhibited by hatchery individuals may not translate into increased survival success in the wild. Results also suggest that a high degree of variability exists within hatcheries and within bay systems. While the exact cause(s) of this variability are not known, it is possible that environmental characteristics, genetics, condition, or selective

forces such as starvation or predation may lead to variation in the survival skills of hatchery and wild red drum. Such variability should be considered when stocking fish or when using pre-release exposure techniques to mitigate behavioral differences between hatchery and wild populations (Conover 1998).

CHAPTER III

THE IMPACT OF HABITAT EXPOSURE AND ONTOGENY ON THE SURVIVAL SKILLS OF HATCHERY RED DRUM

Introduction

Over the past century, increasing demands on recreationally and commercially important fish stocks have lead to severe population declines worldwide. This growing trend has prompted fisheries managers to focus on stock enhancement initiatives to help remedy the current situation. One common form of stock enhancement involves large-scale releases of hatchery-reared individuals in an effort to supplement natural populations (Olla et al. 1998; Welcomme and Bartley 1998; Brown and Laland 2001). While stocking efforts have been reported in over 90 countries (Welcomme and Bartley 1998), the fate of hatchery progeny in natural environments is largely unknown as estimates of survival rates are rarely documented empirically (Blankenship and Leber 1995).

Hatchery fish should demonstrate behaviors similar to that of their wild counterparts (Brown and Laland 2001); however, research has indicated that hatchery individuals exhibit behavioral deficiencies in prey-capture (Suboski and Templeton 1989; Ellis et al. 2002; Wintzer and Motta 2005), anti-predator performance (Suboski and Templeton 1989; Álvarez and Nicieza 2003; Smith and Fuiman 2004), and the ability to use complex habitats (Stunz and Minello 2001; Stunz et al. 2001). These behaviors have been linked to the sensory-deprived hatchery environment, which is typically void of many natural elements (Olla et al. 1998).

Whereas basic survival behaviors may be compromised by the hatchery experience (Munro and Bell 1997), these deficits can be reduced via pre-release exposure to natural stimuli (Jarvi and Uglem 1993; Brown and Laland 2001). Specifically, exposing naïve hatchery fish to predators, mobile prey, or complex habitats prior to release may stimulate the development of certain behavioral traits that improve

survival (Jarvi and Uglem 1993; Brown et al. 2003; Wintzer and Motta 2005; Vilhunen 2006). For example, manipulation of the rearing environment through the addition of complex habitat or structure, also known as environmental enrichment, is thought to promote behavioral flexibility in captive animals (Hunter et al. 2002; Kempermann et al. 2002; Braithwaite and Salvanes 2005). Recent experiments with hatchery cod (*Gadus morhua*) have demonstrated that even simple exposure to complex habitats (e.g., cobble, plastic kelp) aids in the development of feeding and anti-predator behaviors conducive to post-release survival (Braithwaite and Salvanes 2005; Salvanes and Braithwaite 2005). Such findings suggest that the presence of habitat during the rearing experience impacts a range of behaviors in hatchery progeny, many of which are linked to survival success.

In this study, I examined whether pre-release exposure to habitat impacts the development of survival skills in a recreationally important marine species, the red drum (*Sciaenops ocellatus*). Red drum historically supported a thriving commercial fishery in the Gulf of Mexico, and supplemental stocking programs for red drum currently exist in several states in the U.S. (Florida, Texas, South Carolina, Georgia) (Woodward 2000; Smith et al. 2001). To date, experimental evidence has shown that hatchery-reared red drum lack certain survival skills and experience higher mortality than their wild counterparts (Stunz and Minello 2001; Stunz et al. 2001; Smith and Fuiman 2004), and there is concern that this may reduce the effectiveness of supplemental stocking programs. I tested the hypothesis that habitat exposure will enhance survival skills in naïve hatchery red drum since rearing environments often lack structural complexity and there is evidence that the addition of habitat to these areas may enhance survival behaviors in other stocked species (Berejikian et al. 2000, 2001; Braithwaite and Salvanes 2005; Salvanes and Braithwaite 2005). To assess the effect of habitat exposure on survival, a suite of prey-capture and anti-predator performance variables (defined here collectively as 'survival skills') were quantified for fish reared with and without natural vegetation using high-speed video after predetermined exposure periods. Survival skills were quantified at two different intervals (e.g., 10 and 20 days of

exposure) to assess the impact of ontogeny (i.e., age) on prey-capture and anti-predator performance.

Methods

Exposure trials. – Red drum larvae used for experimental trials were obtained from the Texas Parks and Wildlife Department's (TPWD) SeaCenter hatchery (SCT) in Lake Jackson, Texas on 23 June 2005. Red drum at 18 days post hatch (10-12 mm standard length, SL) were collected from a single pond using a dip net and transported to a wet-lab facility in Galveston, Texas. This size was chosen since it parallels the age when wild red drum are fully recruited to estuarine nursery habitats (Rooker et al. 1999). The effect of habitat exposure on performance was evaluated by stocking red drum (35 fish per tank) into fiberglass mesocosms (1.5 m diameter, 0.75 m deep) with and without vegetation (4 replicates per treatment = 8). I used smooth cordgrass (*Spartina alterniflora*) at a shoot density of ~100 stems per m^2 for the vegetated treatment which was a rough approximation of natural densities found in nearby saltmarsh communities. Marsh-edge environments containing smooth cordgrass are commonly used by newly settled red drum in the northern Gulf of Mexico (Baltz et al. 1993; Stunz et al. 2002), and thus represented suitable vegetation for habitat exposure trials. Each mesocosm contained sand approximately 10 cm deep and was filled with sand-filtered seawater pumped from the Gulf (26.5-29.2^{o}C, 32-33 ppt). Red drum were fed a mixture of natural prey (mysid shrimp, Mysidacea spp., < 4 mm total length) and enriched 2-day *Artemia franciscana* once daily throughout the course of the trials. Fish were reared for either 10 or 20 days, after which length (± S.E.) was measured to the nearest 0.01 mm. Lighting was provided by fluorescent bulbs placed on a 12 L:12 D cycle to simulate natural light conditions.

High-speed video analysis. – At day 10 and day 20 of the rearing trials, three individual red drum (n = 3) were sampled at random from each tank and placed into individual chambers (18 cm x 10 cm) for high-speed video analysis. Six prey-capture

performance variables were quantified at both exposure periods: attack distance, mean attack velocity, capture time, maximum gape, time to maximum gape, and gape cycle duration (Table 3). Prey-capture performance was evaluated by recording a series of feeding strikes on mysid shrimp, a natural prey item of red drum at this stage (Soto et al. 1998). The size of mysid shrimp prey used in this experiment was similar across all experimental trials.

Immediately following prey-capture trials, I recorded anti-predator performance of these same individuals using a visual stimulus. The stimulus consisted of a 4.5-cm diameter bulls-eye target on a swinging pendulum arm that was modeled after Batty (1989). This apparatus has been shown to effectively produce an escape response in red drum larvae and juveniles (Fuiman and Cowan 2003; Smith and Fuiman 2004). All anti-predator trials were conducted in a separate control box to minimize the effect of observer influence, and fish were allowed to acclimate for 20 min before the stimulus was introduced. The pendulum was released by the observer when the fish was near the front of the chamber and pointing towards the direction of the stimulus. Preliminary trials indicated that the velocity of the stimulus as it approached the container was approximately 120 cm/s. Six variables were recorded for red drum at day 10 and day 20, including: reaction distance, response distance (distance traveled in 100 ms), maximum velocity, time to maximum velocity, mean velocity, and maximum acceleration (Table 3). Filming began immediately after the stimulus was released, and the pendulum was blocked prior to making contact with the container. During a typical anti-predator event, fish bent sharply to the right or left away from the approaching stimulus (C-start) and swam rapidly towards the opposite end of the container. In many cases, I was unable to analyze an entire anti-predator event since fish either made contact with the sides of the container or swam outside the field of view during the course of an escape event. Therefore, I analyzed only the first 100 ms of each event.

Prey-capture and anti-predator performance of each red drum was filmed at 250 frames per second (fps) using a Redlake MotionScope PCI 1000S high-speed video

Table 3. Variables associated with prey-capture and anti-predator performance in red drum. All variables are referenced to time zero.

Variable	Units	Description .
Prey-capture performance:		
Attack distance	mm	Distance from the tip of the premaxilla to the closest point on the prey at the beginning of prey capture
Mean attack velocity	mm/s	Average red drum velocity from time zero to when the prey completely entered the mouth
Capture time	ms	Time to when the prey completely entered the mouth
Maximum gape	mm	Greatest distance from tip of the premaxilla to the tip of the dentary bone
Time to maximum gape	ms	Time to when maximum gape is reached
Gape cycle duration	ms	Time elapsed from mouth opening to closing
Anti-predator performance:		
Reaction distance	mm	Distance between red drum and center of target at time zero
Response distance	mm	Distance traveled during the first 100 milliseconds of a response
Maximum velocity	mm/s	Maximum velocity reached during a response
Time to maximum velocity	ms	Time to when maximum velocity is reached
Mean velocity	mm/s	Average velocity during a response
Maximum acceleration	mm/s^2	Maximum acceleration reached during a response

camera. Prey-capture events were filmed laterally to the camera and anti-predator events were filmed from above. A 1-cm x 1-cm grid placed behind the fish was used to provide scale during footage analysis. An average of three successful prey-capture and anti-predator events were recorded for each fish (3 trials x 3 fish x 2 habitat treatments x 2 exposure periods). Each fish was given 15-20 min between successive events in order to allow for recovery time and to prevent habituation to the stimulus. Prey-capture and anti-predator footages were saved to a hard drive and analyzed using Redlake MotionScope 2.30.0 and Peak Motus 8.0 software at 2-4x magnification. Each variable was referenced to time zero, corresponding to the frame prior to mouth opening during feeding, and the frame immediately preceding the first movement during an escape response. Velocity and acceleration data were calculated by tracking a digitized point on the center of the eye during prey-capture, and the center of mass during anti-predator events (~30% from tip of snout, verified from preserved specimens). Resulting displacement data were uploaded to QuickSAND (Quick Smoothing and Numerical Differentiation) software for MAC and were smoothed using a generalized cross-validatory (GCV) quintic spline algorithm (Walker 1997). This algorithm has been shown to accurately estimate velocity and acceleration at the frame rate (250 fps) and magnification (2-4x) specified in this study (Walker 1998; Bergmann and Irschick 2006). A second quintic spline with a previously determined mean squared error (MSE) produced similar results to the GCV quintic spline and therefore is not reported.

Data analysis. – Data were tested for normality and equality of variance using Kolgomorov-Smirnov and Levene's tests, respectively. Significant values for three variables (reaction distance, response distance, maximum acceleration) were Ln-transformed to minimize heteroscedascity. Repeated-measures analysis of variance (ANOVA) was used to test for differences in survival skills between rearing habitats (non-vegetated versus vegetated) or days (10 versus 20), since fish from the same tank were not truly independent measures. Repeated-measures were based upon the responses of each of three fish sampled per tank (n = 3) and separate repeated-measures ANOVAs were generated for each prey-capture and anti-predator variable. Initially,

analysis was conducted on the size-removed residuals in order to account for any differences in size. This approach yielded similar results in regards to habitat effect(s), indicating that sizes were comparable across rearing treatments; however, it did not allow us to properly examine day effect(s) or the interaction term (habitat x day). Therefore, analysis of the main effects and interactions were based upon the original data rather than residuals. All statistics were conducted with SPSS statistical software (version 13.0) and $\alpha = 0.05$. Additionally, the amount of inter-individual variability for red drum within each tank (n = 3) was measured for each prey-capture and anti-predator variable. Variability was quantified using the coefficient of variation, expressed as a percentage (CV = S.D. / mean · 100).

Results

Prey-capture performance. – Red drum feeding attempts were successful 87% and 90% of the time for fish reared with and without vegetation, respectively. Prey-capture performance in red drum was highly stereotypical and began with an individual focusing on a particular prey and lunging towards the prey while rapidly opening the mouth. Once the prey entered the mouth, fish would then initiate mouth closure, signifying the end of the feeding event. The duration of each feeding event ranged from 25 to 30 ms, regardless of treatment.

Repeated-measures ANOVA indicated that capture time was the only variable found to be significantly different between habitats; fish reared without vegetation captured prey at a faster rate (~1 ms) than fish reared with vegetation (smooth cordgrass) ($F = 5.030$, df = 1, 12, $P = 0.045$) (Figure 4). While not statistically significant, red drum reared with vegetation exhibited a greater attack distance, mean attack velocity, and time to maximum gape versus individuals reared without vegetation (Figure 4). Mean length (± S.E.) of red drum did not differ between individuals reared with (n = 12) and without vegetation (n = 12) at day 10 (23.04 ± 1.14 and 24.25 ± 1.05 mm; $F = 0.606$, df = 1, 6, $P = 0.466$) or day 20 (32.42 ± 1.62 and 33.29 ± 0.94 mm; $F = 0.217$, df = 1, 6,

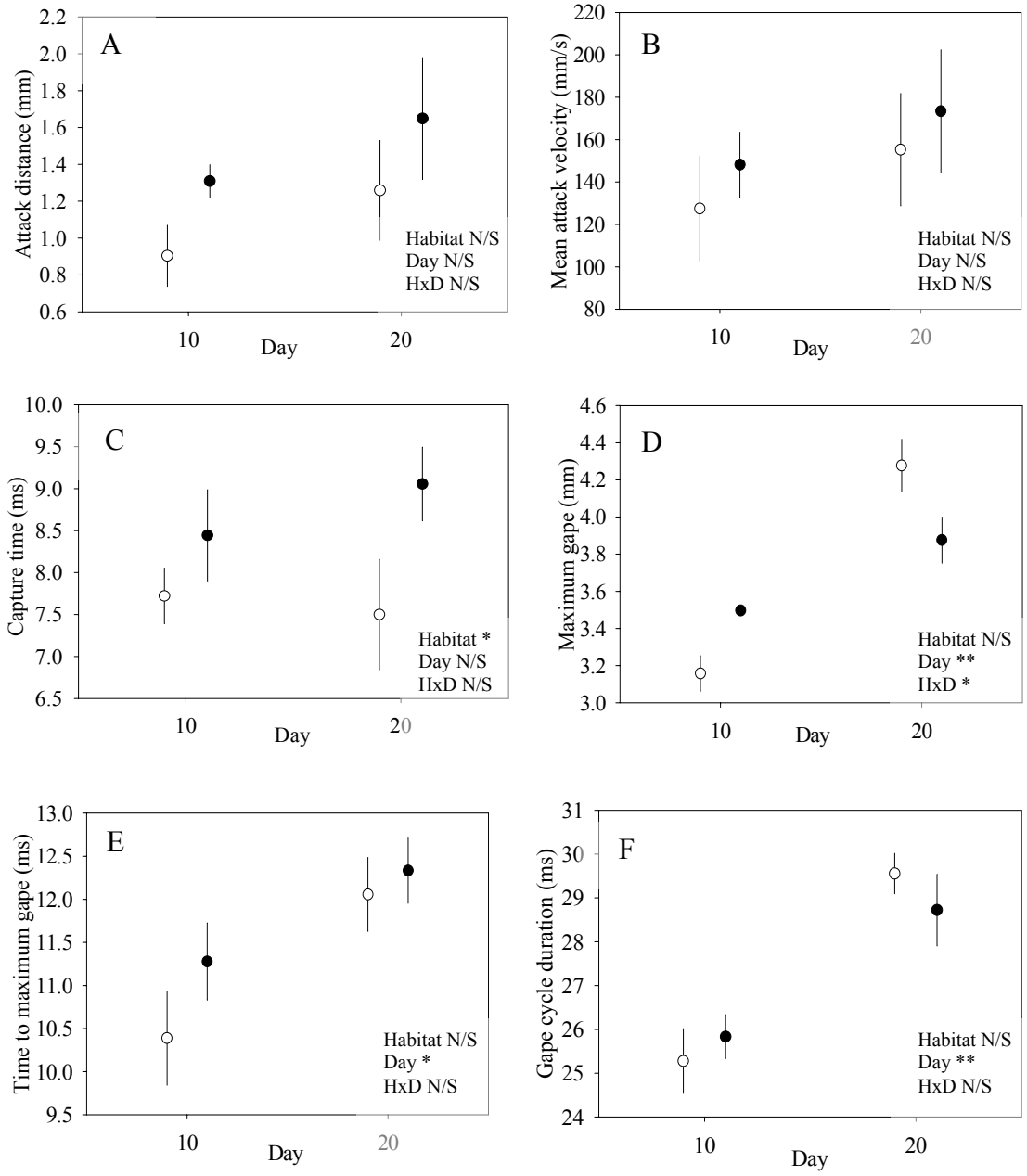

Figure 4. Mean values (± S.E.) of variables associated with prey-capture performance in red drum: (A) attack distance, (B) mean attack velocity, (C) capture time, (D) maximum gape, (E) time to maximum gape, and (F) gape cycle duration. Open circles (○) designate non-vegetated habitats and closed circles (●) designate vegetated habitats. Asterisks represent significant differences between habitats, days and the interaction term (habitat x day). (*$P < 0.05$, **$P < 0.01$)

$P = 0.657$), suggesting that growth was not impacted by exposure to the different habitats. Several performance variables increased in magnitude from day 10 to day 20 in red drum (Figure 4); however, only maximum gape, time to maximum gape, and gape cycle duration were found to be significantly greater in red drum after 20 days of exposure (Figure 4D-F). This finding corresponded to a significant increase in overall length (± S.E.) with ontogeny (i.e., day 10 to day 20) from 23.04 ± 1.14 to 32.42 ± 1.62 mm for fish reared without vegetation (n = 12) ($F = 22.296$, df = 1, 6, $P = 0.003$) and 24.25 ± 1.05 to 33.29 ± 0.94 mm for fish reared with vegetation (n = 12) ($F = 41.161$, df = 1, 6, $P = 0.001$). A significant interaction effect (habitat x day) was detected for maximum gape ($F = 12.236$, df = 1, 12, $P = 0.004$). Fish reared in vegetation had a greater maximum gape after 10 days of exposure, while the same was true for fish from non-vegetated habitats after 20 days (Figure 4D). Additionally, the coefficient of variation (CV) ranged from 0.0 – 101.3% for prey-capture variables, indicating a high level of variability among individuals (Table 4). Maximum gape, time to maximum gape and gape cycle duration exhibited the lowest CVs (≤ 20%), while values for attack distance, mean attack velocity and capture time were typically higher (≥ 20%).

Anti-predator performance. – Red drum exhibited a typical C-start escape maneuver in response to the approaching predator stimulus. When the stimulus was recognized, fish bent sharply about their center of mass away from the stimulus and accelerated forward with a single propulsive tail stroke, followed by continuous burst swimming activity.

Repeated-measures ANOVA indicated that reaction distance and time to maximum velocity were significantly greater for fish reared without vegetation (Figure 5). Reaction distance for fish from non-vegetated habitats was nearly twice the distance of that reported for individuals reared in vegetation ($F = 8.555$, df = 1, 12, $P = 0.013$). Additionally, time to maximum velocity was as much as 40% longer for fish reared in non-vegetated habitats ($F = 8.140$, df = 1, 12, $P = 0.015$). No effect of habitat was detected for the remaining anti-predator performance variables (response distance, maximum velocity, mean velocity, and maximum acceleration) (Figure 5).

Table 4. Variability in performance for prey-capture and anti-predator variables among red drum within each tank (n = 3) as measured by the coefficient of variation (CV = S.D. / mean · 100). T1 = tank 1, T2 = tank 2, etc.

	w/ Vegetation								w/o Vegetation							
	Day 10				Day 20				Day 10				Day 20			
Variable	T1	T2	T3	T4	T1	T2	T3	T4	T1	T2	T3	T4	T1	T2	T3	T4
Prey-capture performance:																
Attack distance (mm)	48.3	37.4	66.4	97.9	71.7	24.2	101.3	18.2	38.9	79.9	57.5	33.0	68.9	44.9	61.4	99.5
Mean attack velocity (mm/s)	21.9	39.9	52.0	39.1	52.3	55.5	83.4	33.3	47.5	69.3	64.9	37.6	56.0	43.3	56.9	63.4
Maximum gape (mm)	2.9	10.9	17.9	14.7	16.3	11.8	9.4	9.5	15.6	13.0	2.4	5.8	15.3	14.8	18.0	17.7
Time to maximum gape (ms)	10.2	16.3	6.7	0.0	20.0	6.7	6.2	0.0	14.5	20.0	0.0	20.0	18.6	10.0	14.2	6.7
Capture time (ms)	32.7	21.7	28.6	44.1	28.6	30.1	20.8	24.7	9.1	25.0	10.2	14.8	31.2	16.7	15.8	53.3
Gape cycle duration (ms)	4.3	7.9	3.2	11.9	11.6	8.9	7.5	4.0	3.2	0.0	8.8	9.1	7.9	2.6	3.8	2.7
Anti-predator performance:																
Reaction distance (mm)	107.8	37.3	90.5	76.1	21.4	73.7	82.3	31.8	33.7	19.3	110.1	47.1	23.8	77.0	47.4	11.9
Response distance (mm)	3.7	24.6	22.9	17.6	57.2	37.8	28.4	23.7	56.2	45.5	31.2	6.8	78.5	4.4	23.5	12.1
Maximum velocity (mm/s)	11.5	40.3	41.3	26.5	57.1	32.4	20.8	31.1	31.8	39.5	22.5	24.6	63.5	27.7	6.3	32.6
Time maximum velocity (ms)	10.8	52.3	57.6	78.7	7.3	18.4	56.9	41.8	14.9	18.9	44.7	41.9	35.9	34.3	25.2	35.7
Mean velocity (mm/s)	3.7	25.8	22.7	11.1	57.6	37.5	28.2	34.6	54.4	44.8	30.9	3.4	78.6	4.6	23.5	12.0
Maximum acceleration (mm/s^2)	47.2	56.7	70.9	50.5	75.6	42.6	37.4	11.3	43.7	58.2	26.5	51.7	61.3	74.7	73.4	69.0

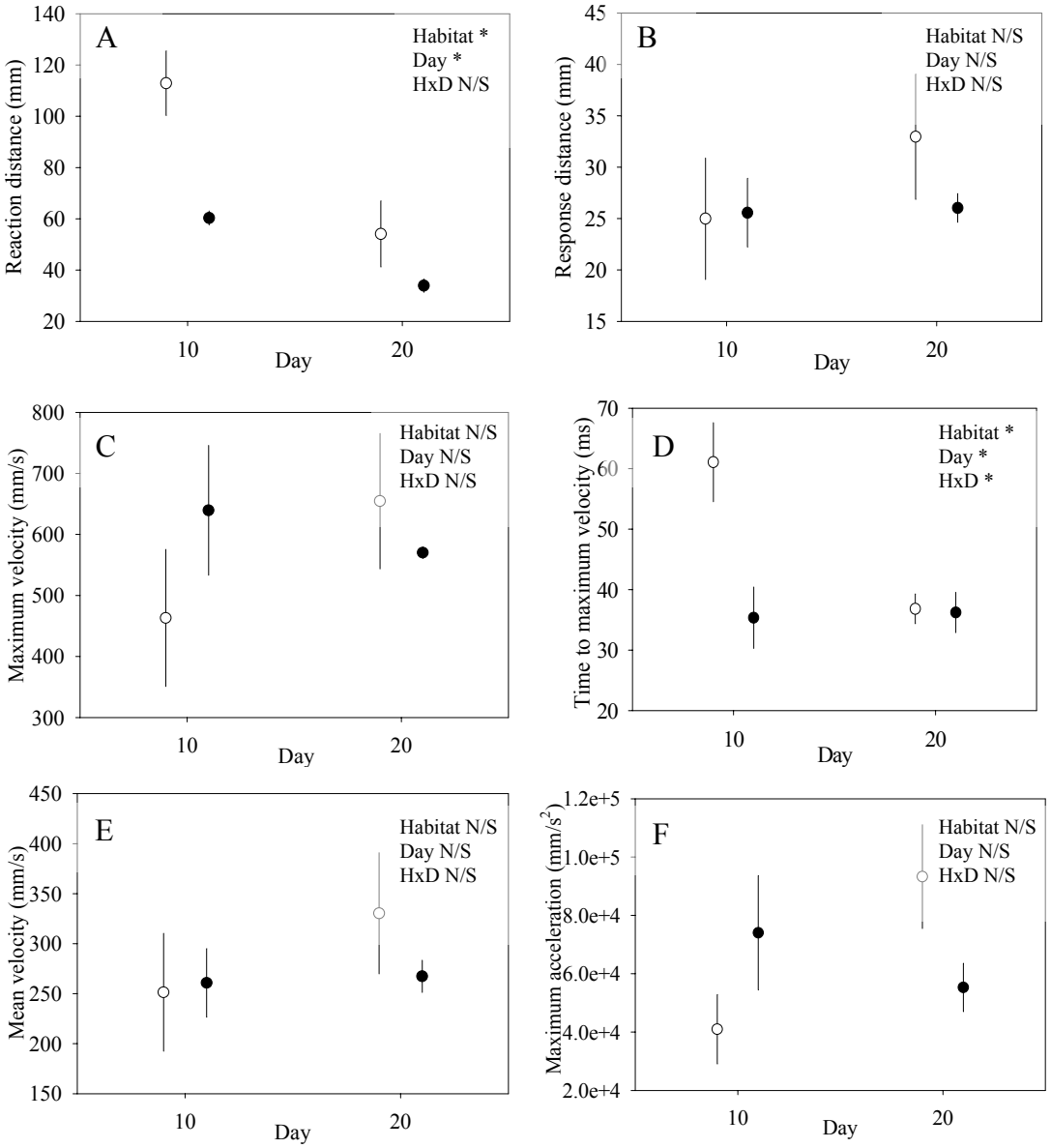

Figure 5. Mean values (± S.E.) of variables associated with anti-predator performance in red drum: (A) reaction distance, (B) response distance, (C) maximum velocity, (D) time to maximum velocity, (E) mean velocity, and (F) maximum acceleration. Open circles (○) designate non-vegetated habitats and closed circles (●) designate vegetated habitats. Asterisks represent significant differences between habitats, days and the interaction term (habitat x day). (*$P < 0.05$, **$P < 0.01$)

Mean reaction distance decreased by as much as 50% from day 10 to day 20 for fish reared with (n = 12) and without vegetation (n = 12) ($F = 10.990$, df = 1, 12, $P = 0.006$) (Figure 5A). Likewise, time to maximum velocity decreased approximately 40% from day 10 to day 20, although this trend only occurred for fish in the non-vegetated habitat ($F = 6.478$, df = 1, 12, $P = 0.026$) (Figure 5D). Statistical tests for the remaining four variables were not significantly different; however, interaction effects of day and habitat were detected for time to maximum velocity ($F = 7.532$, df = 1, 12, $P = 0.018$). Time to reach maximum velocity was ca. 40% longer after 10 days versus 20 days of exposure for fish reared in non-vegetated habitats, but time to maximum velocity remained consistent between these exposure periods for fish reared in vegetation (Figure 5D). The coefficient of variation (CV) ranged from 3.4 – 110.1% for anti-predator variables (Table 4). Overall, CVs were ≥ 20% for the majority of variables tested; however, CVs were highest for reaction distance and maximum acceleration.

Discussion

Analysis of red drum feeding events indicated that prey-capture performance was not significantly improved by exposure to *Spartina* spp. (smooth cordgrass) vegetation. Red drum exhibited similar feeding behaviors when capturing mysid shrimp prey, with the exception of capture time, which occurred an average of 1 ms slower in fish reared in vegetation. Although longer capture times may negatively impact feeding performance by increasing the possibility of prey escape, this did not appear to impact feeding ability in red drum as the percentage of successful prey-capture attempts was approximately 90%, regardless of treatment.

Previous studies have demonstrated a negative relationship between feeding performance in fishes and increasing habitat complexity. For example, mummichog, *Fundulus heteroclitus* (Heck and Thoman 1981), largemouth bass, *Micropterus salmoides* (Savino and Stein 1982), pinfish, *Lagodon rhomboides* (Minello and Zimmerman 1983), razorfish, *Pelecus cultratus* (Tátrai and Herzig 1995), and stone moroko, *Pseudorasbora parva* (Manatunge et al. 2000) have all shown reduced foraging

efficiency (e.g., number of prey captured) in more structurally complex environments. In some cases, the number of prey consumed decreased by up to 50% in areas of high cover (Heck and Thoman 1981), although the overall effect of structure on feeding success varies among species (Minello and Zimmerman 1983; Winfield 1986). It should be noted that this study examined red drum prey-capture performance in non-vegetated areas but previous evidence suggests that the presence or absence of vegetation has little impact on red drum predation rates (Minello and Zimmerman 1983). As a result, it is likely that red drum feeding behaviors will remain consistent, regardless of the presence of habitat.

Ontogeny had a pronounced effect on prey-capture performance in red drum. Maximum gape was larger in older red drum (20 days of exposure), corresponding to a significant increase in overall size (Richard and Wainwright 1995; Cook 1996; Hernández 2000; Huskey 2003). Larger gape would allow these individuals to exploit a wider range of prey items (Krebs and Turingan 2003), and possibly lead to a competitive advantage over younger, smaller red drum as well as other fishes. Conversely, time to reach maximum gape and gape cycle duration were longer for older red drum, likely resulting from a reduction in muscle contraction velocity with age (Richard and Wainwright 1995). As mentioned previously, slower feeding events may negatively affect prey-capture performance, yet there was no indication of this during filming trials as the majority of feeding strikes (~90%) resulted in successful prey acquisition. It is noteworthy that red drum reared in vegetation had a larger gape than fish from non-vegetated tanks after 10 days of exposure, while this trend was reversed after 20 days. While the reason for this is not clear, slight size differences among fish from vegetated and non-vegetated tanks may have resulted in a significant interaction term (habitat x day) for this variable. In addition to overall differences among habitat and day treatments, a high level of variability in prey-capture performance was observed for red drum within each tank. This was most apparent for attack distance, mean attack velocity and capture time where CVs were typically $\geq 20\%$, regardless of tank. By contrast, CVs were lower ($\leq 20\%$) for maximum gape, time to maximum gape and gape cycle duration.

Since timing and distance of cranial elements are closely linked to size (Richard and Wainwright 1995), low CVs for these variables may reflect the restricted size range of individuals within each treatment.

Anti-predator behaviors in red drum were consistent with the typical Mauthner-initiated response described for fishes (Eaton et al. 1991). In general, escape reactions of red drum reared with and without vegetation appeared to be similar for the majority of variables measured. Still, individuals reared in vegetation consistently demonstrated a shorter reaction distance to the visual stimulus. Reaction distance determines the amount of time that prey would have to fully execute escape maneuvers and reach safety (Dill 1974). For example, reacting too late (short reaction distance) may reduce the chances of prey escape, while reacting too soon (long reaction distance) could also provide the opportunity for predators to correct their path of attack, thereby influencing capture probability. Previously, Grant and Noakes (1987) demonstrated that reactive distance of young-of-the-year brook trout, *Salvelinus fontinalis*, was shorter for fish that were located in close proximity to vegetation. It was hypothesized that these fish adjusted their reactive distance based on the risk of predation, as approaching predators were seen as less threatening when cover was nearby (Grant and Noakes 1987). It is possible that red drum reared in vegetation also increased their reaction distance as a result of exposure to vegetation. Alternatively, exposure to vegetation may have simply resulted in red drum being less perceptive to their surroundings, and thus less responsive to the approaching stimuli, particularly since red drum from vegetated tanks typically dispersed among vegetative clusters in comparison to red drum in non-vegetated tanks, which often schooled in larger groups and displayed increased swimming activity. Interestingly, while reaction distance was shorter for red drum reared in vegetation, time to maximum velocity was generally more rapid for these individuals, suggesting that these fish may attempt to compensate for their latency in response by maximizing their swimming speed at a faster rate. This was most apparent after 10 days of exposure, with red drum reared in vegetation reaching maximum velocity approximately 40% faster than fish from non-vegetated tanks. After 20 days of exposure, this difference was

almost negligible (< 1%), as red drum from both vegetated and non-vegetated tanks typically attained maximum velocity at 36 ms into the response.

Ontogeny also appeared to be a significant factor in determining the extent of anti-predator performance exhibited by red drum. Since visual acuity improves during ontogeny (Breck and Gitter 1983; Poling and Fuiman 1999), older fish should have larger reaction distances compared to younger individuals. Nevertheless, I observed a decrease in red drum reaction distance by almost half from day 10 to day 20 of exposure. Age may have impacted motivation and physiology in red drum, as suggested by Braithwaite and Salvanes (2005) who found that cod (*G. morhua*) reared in heterogeneous environments for 20 weeks took longer to recover their opercular beat rate following a simulated predator attack versus individuals reared for 14 weeks. Still, there is the possibility that the extended rearing time (20 days) may have compromised anti-predator behaviors in some way that was not measured during filming trials (e.g., declining health caused by 'conditioning' to an artificial environment). Time to maximum velocity also decreased in older red drum; however, this difference was only witnessed for red drum reared in non-vegetated tanks. Swimming performance in fishes generally improves with age, concurrent with development of the fins and increased muscle capacity (Webb and Weihs 1986; Goolish 1989; Osse and van den Boogaart 1999; Ojanguren and Braña 2003). The ability of older red drum to achieve maximum velocity at a faster rate reflects this trend and may help reduce predator efficiency on these individuals by allowing fish to move more of their body outside of the predator's gape path during an attack sequence (Paglianti and Domenici 2006). As was the case with prey-capture, a high degree of variability in anti-predator performance was also witnessed among red drum within each tank. In general, CVs were ≥ 20% for each of the six variables tested, although these values were highest for both reaction distance and maximum acceleration. High levels of inter-individual variability may reflect the genetic diversity of the population since individuals were spawned from multiple adults (2-3 females and 2-3 males per tank, 8 tanks) at SCT. Alternatively, differences in condition (e.g., gut fullness, RNA:DNA) among individuals may have also influenced

CVs, yet this was not directly examined. The amount of variability in this study was relatively large compared to the inter-individual variability in critical swimming velocity (U_{crit}) reported for wild Atlantic salmon, *Salmo salar* (9.9 – 35.4%, Reidy et al. 2000). Abundant food reserves and lack of predators in the hatchery environment may allow the persistence of poorer performing individuals, therefore, the range of CVs reported here are likely not consistent with that found in wild red drum populations.

In conclusion, two major findings in regards to pre-release exposure in red drum were observed: 1) habitat exposure does not substantially improve survival skills in red drum, and 2) survival skills associated with prey-capture and anti-predator performance vary with ontogeny. Exposure to vegetation had little influence on prey-capture in red drum, yet several anti-predator variables decreased in magnitude as a result of this exposure. This trend was most apparent for reaction distance, suggesting that fish reared in vegetation may be less responsive to an approaching stimulus, perhaps because these individuals would be able to find shelter quickly when threatened. Consequently, I suggest that hatchery releases of red drum should be conducted in close proximity to vegetated areas, regardless of the condition of hatchery tanks. Ontogenetic effects on red drum survival skills were substantial, and several prey-capture variables were found to increase with size. Conversely, several anti-predator variables including reaction distance and time to maximum velocity decreased from day 10 to day 20, indicating that older fish may not be as responsive to an approaching stimulus as younger individuals. Further experiments should be conducted to determine whether these differences occurred due to increasing size, age or extended rearing periods. Another important aspect to this study was that high levels of variability in performance were witnessed among individuals from the same tank. Although this may be linked to genetic diversity or condition, it also suggests the presence of individuals which may possess poorly developed survival skills. Such individuals may be problematic for stocking efforts as they could fall victim to starvation and predation pressures shortly after release.

Overall, red drum reared in vegetation after 10 days appeared to perform better than fish from all other treatments for prey-capture and anti-predator behaviors. For

example, red drum reared in vegetation achieved similar behavioral levels earlier (day 10) than fish from non-vegetated tanks. Additionally, the response of red drum reared in vegetation appeared to diminish over time. Based on this evidence, I suggest that red drum should be reared in vegetated tanks and released earlier in order to solidify any survival benefits gained by habitat exposure. Finally, I suggest that future pre-release exposure trials incorporate the use of other natural elements (e.g., predators, prey types) in addition to complex habitat to determine if a combination of stimuli will further enhance survival behaviors in hatchery red drum.

CHAPTER IV

EFFECT OF PREDATOR EXPOSURE ON THE PERFORMANCE AND SURVIVAL OF HATCHERY RED DRUM

Introduction

During early life marine teleosts typically experience high levels of predation-related mortality, often resulting in significant losses to a cohort (Houde 1987). Predation is a strong selective force, and its pervasiveness over the course of an individual's lifetime has led to the development of various anti-predator defenses. Many of these defenses are behavioral in nature, including the ability to 'freeze' (Jarvi and Uglem 1993; Brown and Smith 1998; Lehtiniemi 2005), bury (Howell and Baynes 1993; Kellison et al. 2000), school (Seghers 1974; Pitcher and Parrish 1993) or use habitat refugia (Sogard and Olla 1993; Katz and Dill 1998) when a predatory threat arises. Fish react to predatory threat based upon visual (Helfman 1989; Engström-Öst and Lehtiniemi 2004), chemical (Magurran 1989; Chivers and Smith 1994a; Kristensen and Closs 2004), and/or mechanosensory cues (Blaxter and Fuiman 1990; Fuiman 1994). While such behaviors are often considered to be genetically based (Patten 1977; Giles 1984), increasing evidence suggests that anti-predator responses are often learned or modified with experience (Magurran 1990; Magurran and Seghers 1990; Kelley and Magurran 2003).

The ability of fish to 'learn' to respond to predatory threat is of particular interest to hatchery managers since fish produced for supplemental stocking are often deficient in their ability to detect and avoid predators (Olla et al. 1998). It has been argued that these deficits arise as a result of the lack of predatory stimuli in the rearing environment (Olla et al. 1998), resulting in the production of naïve progeny that experience high rates of mortality following release (Kristiansen et al. 2000; Brown and Laland 2001). Previous studies have demonstrated that pre-release exposure to predatory stimuli, whether visual (Olla and Davis 1989; Suboski and Templeton 1989; Jarvi and Uglem

1993) or chemical (Brown and Smith 1998; Vilhunen 2006), may significantly enhance anti-predator behaviors and overall survival in captive-reared species. Nevertheless, few fisheries managers have applied such techniques to hatchery-release programs and many questions remain regarding the proper methods and circumstances under which they should be implemented (Brown and Laland 2001).

The purpose of this study was to determine whether pre-release exposure to predators impacts the survival of hatchery red drum, *Sciaenops ocellatus*. Red drum is an important recreational species in the U.S. and is currently the focus of several large-scale stock enhancement programs in the Gulf of Mexico and parts of the eastern seaboard (Smith et al. 2001). In Texas alone, over 460 million red drum fingerlings have been stocked into local bays and estuaries by the Texas Parks and Wildlife Department (TPWD) since the early 1980's (Robert R. Vega, TPWD, personal communication); however, there is little evidence that these fish enhance natural populations (Scharf 2000). In both laboratory (Rooker et al. 1998; Stunz and Minello 2001) and field studies (Serafy et al. 1999), hatchery red drum have been shown to experience high rates of predation. These individuals have also demonstrated deficiencies in behaviors associated with predator detection and avoidance (Smith and Fuiman 2004), and this may be linked to the absence of predators in the rearing environment. This study tested the hypothesis that pre-release exposure to predators will impact survival in hatchery red drum. Prey-capture and anti-predator performance (i.e., survival skills) of hatchery red drum reared with and without exposure to pinfish (*Lagodon rhomboides*) predators were examined using high-speed video. Additionally, mortality experiments using free-ranging pinfish predators were conducted in order to quantify the rate of instantaneous hourly mortality (Z) experienced by individuals with and without predator exposure.

Methods

Predators and prey. – Red drum were obtained from the Texas Parks and Wildlife Department's (TPWD) SeaCenter (SCT) hatchery in Lake Jackson, Texas on 25

May 2006. These fish were spawned from SCT broodstock (2-3 females and 2-3 males per tank, 8 tanks) under artificial temperature and photoperiod regimes. Fertilized eggs were collected and reared in 12,000-l tanks until three days post hatch (dph), when they were transferred to a 2-acre polyethylene lined pond at SCT. Fish used in this study were collected during harvesting and randomly sampled from transport trailers. Individuals were 25-30 mm standard length (SL), encompassing current TPWD release sizes for this species. Fish were immediately transported to a wet-lab in Galveston, Texas, where they were stocked into fiberglass tanks (1.5 m diameter, 0.75 m deep) containing sand-filtered water (26.5-29.2^{o}C, 30-32 ppt) pumped from the Gulf of Mexico. Fish were fed a mixture of commercial pellet diets, mysid shrimp (Mysidacea spp., < 4 mm total length) and 2 and 3 day post hatch brine shrimp (*Artemia franciscana*) enriched with Algamac 2000 (www.algamac.com) once daily.

Pinfish (80-100 mm SL) were used as predators in this study since evidence has shown that they are natural predators of red drum larvae and juveniles (Fuiman 1994; Rooker et al. 1998). Pinfish were collected from Galveston Bay, Texas, using a 50-foot bag seine and transferred to separate tanks at the wet-lab in Galveston. Pinfish were fed a mixture of live and dead shrimp once daily to satiation, with food being withheld for 24 h prior to the start of all trials to encourage active feeding during exposure periods. Predators were held for less than 1 wk before use in experiments to minimize the impact of captivity on behavior.

Predator exposure trials. – Twenty-four hours after collection, red drum were stocked into twelve separate tanks at a density of 100 fish per tank (~88 fish per m^3). Tanks represented three treatments: with predator, without predator, and control (sweep) (3 treatments x 4 replicates = 12 tanks). A seine net (1.5 m x 1.5 m) was used three to four times in each 'control' (sweep) treatment in order to mimic the disturbance caused by capturing pinfish, while those treatments designated as 'without predator' were left undisturbed. Pre-trial experiments indicated that pinfish exhibited normal feeding behaviors only when placed with another conspecific, and pinfish dramatically reduced feeding levels on red drum after 1 h. As a result, two free-ranging predators were

introduced into 'with predator' treatments for a 1 h period over the course of five days. New predators were used for each trial to reduce any variability which could be attributed to learning effects. On the last day of exposure trials, a mechanical malfunction resulted in loss of a line of tanks. As a result, only three of the four original replicates per treatment were available for the final analysis (3 treatments x 3 replicates = 9 tanks).

After exposure trials had been completed, three red drum (n = 3) were randomly selected from each tank and placed into separate chambers (18 cm x 10 cm) containing 3 cm of seawater. Following a 4-6 h acclimation period, anti-predator performance behaviors were quantified using a high-speed (250 frames per second, fps) videocamera (Redlake MotionScope PCI 1000S). A 1-cm x 1-cm grid placed behind each individual was used to provide scale during all filming events. Prey-capture performance was evaluated by filming individual red drum feeding on live mysid shrimp, a major prey item for red drum larvae and juveniles (Soto et al. 1998). Several mysid shrimp were released into the chamber at a time and only those feeding events during which red drum fed at a lateral angle to the camera and remained in focus throughout the entire event were used in the final analysis. Four prey-capture variables were quantified: 1) attack distance, distance from the tip of the premaxilla to the closest point on the prey at the beginning of prey capture (mm), 2) mean attack velocity, average red drum velocity from time zero to when prey completely entered the mouth (mm/s), 3) capture time, time to when prey completely entered the mouth (ms), and 4) gape cycle duration, time elapsed from time zero to when mouth closes (ms).

Anti-predator performance of each red drum was recorded while responding to a visual stimulus. The stimulus consisted of a 4.5-cm diameter bulls-eye target on a swinging pendulum arm that was modeled after Batty (1989). This stimulus has previously been shown to effectively produce escape responses in red drum larvae and juveniles (Fuiman and Cowan 2003; Smith and Fuiman 2004). Each chamber was placed within a separate control box and red drum were allowed to acclimate to the chamber for 20 min before the stimulus was introduced. Anti-predator events were

filmed from above and began when the red drum was near the front of the container and facing less than 90º toward the direction of the stimulus. When the red drum was in this position, the observer released the stimulus, sending it towards the fish but blocking it prior to making contact with the chamber. In many cases, red drum either made contact with the sides of the container or swam outside the field of view during the course of an escape event; therefore, only the first 100 ms of each event was analyzed. At least 15 min were allowed between anti-predator responses for each individual to prevent habituation to the stimulus. Four anti-predator variables were quantified: 1) reaction distance, distance between red drum and center of target at time zero (mm), 2) response distance, distance traveled during the first 100 ms of response (mm), 3) mean velocity, averaged velocity over the duration of response (mm/s), and 4) maximum velocity, maximum velocity reached during response (mm/s). After the completion of filming trials, red drum were immediately anesthetized with tricaine methanesulfonate (MS-222) and lengths of each fish were measured to the nearest 0.01 mm.

An average of three prey-capture and three anti-predator events were recorded for each red drum (3 trials x 3 fish x 3 treatments). These events were saved to a hard drive and analyzed at 2-4x magnification using Redlake MotionScope 2.30.0 and Peak Motus 8.0 software. Prey-capture events were referenced to time zero, corresponding to the frame prior to mouth opening during feeding, and the frame immediately preceding the first movement away from the stimulus during anti-predator events. Velocity measures were calculated by tracking a digitized point on the center of the eye during prey-capture events, and the center of mass during anti-predator events (~30% from tip of snout, verified from preserved specimens). A generalized cross-validatory (GCV) quintic spline algorithm was applied to the displacement data using QuickSAND (Walker 1997) for accurate velocity measurements. This algorithm has been shown to accurately estimate velocity at the frame rate (250 fps) and magnification (2-4x) used in this study (Walker 1998; Bergmann and Irschick 2006).

Mortality experiments (Z). – Mortality experiments were conducted according to the protocol outlined in Rooker et al. (1998). Twenty red drum were randomly selected

from each tank and placed into separate tanks (3 treatments x 3 replicates = 9 tanks) at 1600 hours and allowed to acclimate for 15 h before mortality experiments began. At 0700 hours the next day, two pinfish predators were released into each tank. After a 6 h period, pinfish were removed using a seine net and the number of surviving red drum was recorded. The remaining red drum were then captured and anesthetized with tricaine methanesulfonate for measurement purposes (MS-222). Each tank was drained and refilled with water to remove any chemical alarm cues before beginning the next set of trials. Three mortality experiments were conducted for a total of 9 replicates per treatment and recovery trials were conducted after the final mortality experiment in order to determine the recovery rate of red drum in the absence of pinfish predators (Rooker et al. 1998). The protocol for the recovery trials was the same as the predation experiments with the exception that no pinfish were used. Due to limited numbers of remaining red drum, only one set of recovery trials was conducted (3 treatments x 3 replicates x 1 trial).

Data analysis. – All data were tested for normality and homogeneity of variances using Kolgomorov-Smirnov and Levene's tests, respectively. Data were regressed against length for each red drum in order to account for any differences in size. Repeated-measures analysis of variance (ANOVA) was conducted on the size-removed residuals for each variable since red drum within the same tank were not truly independent measures. Analysis of variance for each variable on the tank means, i.e., average response of three individuals per tank, gave similar results to repeated-measures ANOVA; therefore, results are restricted to repeated-measures ANOVA.

The following equation was used during mortality experiments to estimate instantaneous hourly mortality (Z $h^{-1} \cdot$ $predator^{-1}$):

$$Z = [\mathrm{Ln}\,(N_i / N_f) - \mathrm{Ln}\,(N_i / N_c)] / T \cdot P \qquad (1)$$

where N_i indicates the initial number of prey stocked within each tank, N_f is the final number of prey recovered, N_c is the mean number of prey recovered from tanks with no

predators (N_c was 20 red drum or 100% for all recovery trials), T is the duration of the experiment in hours, and P is the number of predators added to each tank. This equation was the same used by Rooker et al. (1998). One-way ANOVA was used to test for differences in the instantaneous hourly mortality (Z) among treatment groups (with predator, without predator, control).

In the event that a significant treatment effect was detected for either predator exposure trials or mortality experiments, Tukey's HSD post hoc test was used to determine which factor levels differed from one another. Additionally, the amount of inter-individual variability for red drum within each tank (n = 3) was measured for each prey-capture and anti-predator variable. Variability was quantified using the coefficient of variation, expressed as a percentage (CV = S.D. / mean · 100). All statistics were conducted with SYSTAT (version 12.0) and SPSS (version 13.0) statistical software and $\alpha = 0.05$.

Results

Predator exposure trials. – Pinfish began actively pursuing red drum prey within 5-10 min after release. Red drum reared with predators responded to predatory attacks by schooling at the surface and becoming mottled in coloration, indicating that fish were in distress. Such behaviors were not observed for individuals from tanks without predators. On average, 2 to 5 red drum were consumed by pinfish during the 1 h exposure periods. To keep densities consistent across all treatments as well as to reduce any 'culling' effects on behavioral performance (Patten 1977; Olla et al. 1992), several red drum were randomly removed from without predator and control tanks following each exposure period. Final red drum lengths (± S.E.) were 30.33 ± 0.29 mm (with predator), 29.06 ± 0.58 mm (without predator), and 29.83 ± 1.04 mm (control) and no significant differences in length were found among treatments ($P = 0.482$). The amount of inter-individual variability (CV) was high, ranging from 3.8 – 98.9% and 3.3 – 88.8% for prey-capture and anti-predator performance variables, respectively (Table 5).

Table 5. Variability in prey-capture and anti-predator performance variables for hatchery red drum within each tank (n = 3) as measured by the coefficient of variation (CV = S.D. / mean · 100).

	w/ Predator			w/o Predator			Control		
Variable	Tank 1	Tank 2	Tank 3	Tank 1	Tank 2	Tank 3	Tank 1	Tank 2	Tank 3
Prey-capture performance:									
Attack distance (mm)	33.2	57.2	98.9	33.5	31.5	27.7	91.8	8.4	28.7
Mean attack velocity (mm/s)	14.0	43.9	28.8	35.9	64.9	34.7	47.5	28.6	52.7
Capture time (ms)	17.3	11.9	35.3	13.9	10.2	20.0	28.6	19.9	17.6
Gape cycle duration (ms)	3.8	8.3	21.8	4.5	17.3	22.9	15.4	12.0	4.6
Anti-predator performance:									
Reaction distance (mm)	27.4	88.8	59.5	11.5	35.8	45.4	7.1	38.8	8.3
Response distance (mm)	42.4	57.6	28.1	29.9	36.5	28.3	15.7	43.1	8.6
Mean velocity (mm/s)	41.7	58.9	26.2	29.1	37.0	30.5	16.3	43.1	10.2
Maximum velocity (mm/s)	38.9	65.5	25.9	3.3	9.7	17.1	8.0	26.4	12.8

Prey-capture performance. – Red drum prey-capture attempts were successful ≥ 95% of the time, regardless of treatment. Attack distance ($F = 7.223$, df = 2, 6, $P = 0.025$) and gape cycle duration ($F = 6.013$, df = 2, 6, $P = 0.037$) differed significantly among treatment groups. Tukey's HSD test found that red drum reared with predators had approximately 2x greater attack distance than those reared without predators (Tukey, df = 2, 6, $P = 0.022$), while individuals from control treatments exhibited longer gape cycle duration (5 ms) than those reared without predators (Tukey, df = 2, 6, $P = 0.031$) (Figure 6A, D). Mean attack velocity ($P = 0.158$, power = 0.331) and capture time ($P = 0.249$, power = 0.242) did not differ significantly among treatments; however, both variables were greatest for red drum reared with predators (Figure 6).

Anti-predator performance. – No significant differences among treatment groups were found for reaction distance ($P = 0.387$, power = 0.167), response distance ($P = 0.188$, power = 0.295), mean velocity ($P = 0.197$, power = 0.286), or maximum velocity ($P = 0.212$, power = 0.272). Nevertheless, mean values for all four variables were noticeably greater for red drum reared with predators (Figure 7). In particular, reaction distance of red drum reared with predators was almost 3x greater than that of red drum reared without predators (Figure 7A). Response distance, mean velocity, and maximum velocity of red drum from predator treatments were also 20 – 30% greater for individuals reared with predators (Figure 7B-D).

Mortality experiments (Z). – Instantaneous hourly mortality (Z) rates of hatchery red drum did not differ significantly among treatments ($P = 0.840$, power = 0.067). Overall, mean Z (± S.E) for the three predation experiments were 0.056 ± 0.009, 0.047 ± 0.015, and 0.060 ± 0.020, for with predator, without predator, and control treatments, respectively. Daily Z rates were highly variable among replicates as well as days (Figure 8). For example, red drum reared without predators experienced greater mortality rates compared to red drum reared with predators on day 1, yet this trend was reversed on day 2 and day 3 (Figure 8).

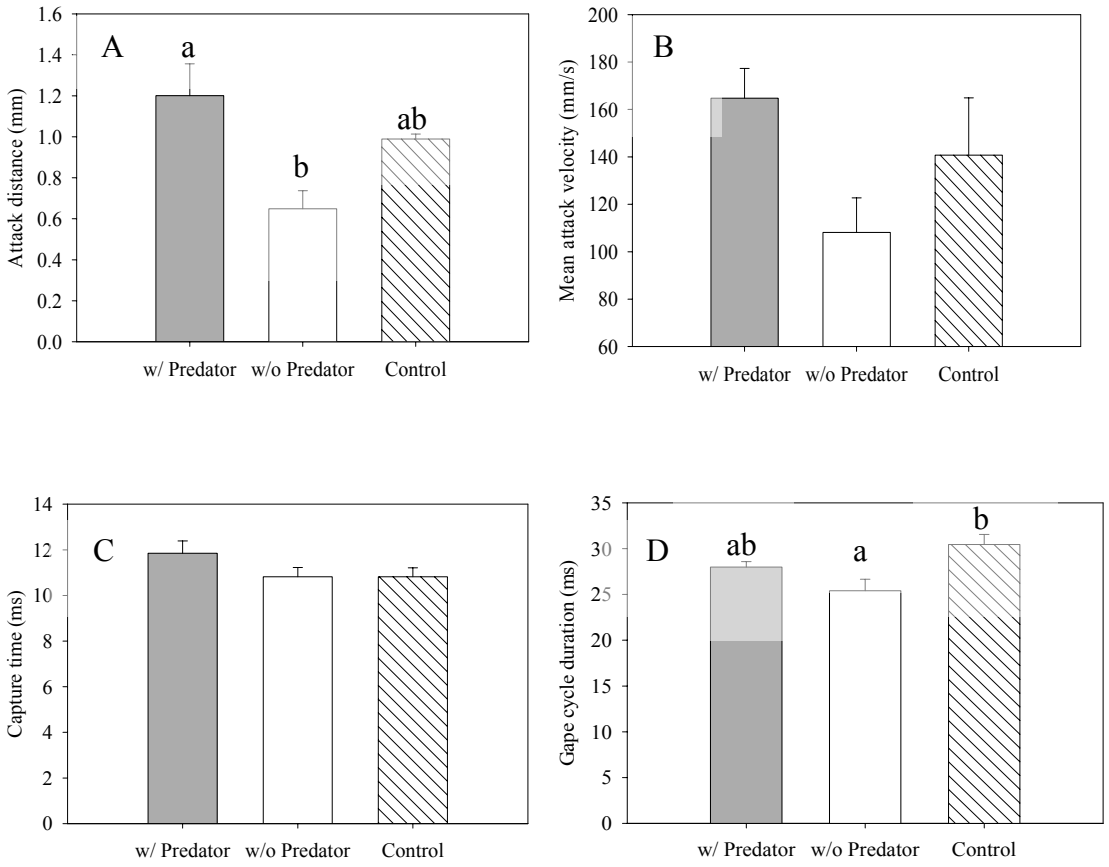

Figure 6. Mean (± S.E.) for prey-capture performance variables in red drum: (A) attack distance, (B) mean attack velocity, (C) capture time, and (D) gape cycle duration. Lower case letters represent significant differences based on Tukey's HSD post hoc tests ($P < 0.05$). Treatments = ■, with predator; □, without predator; ⧅, control.

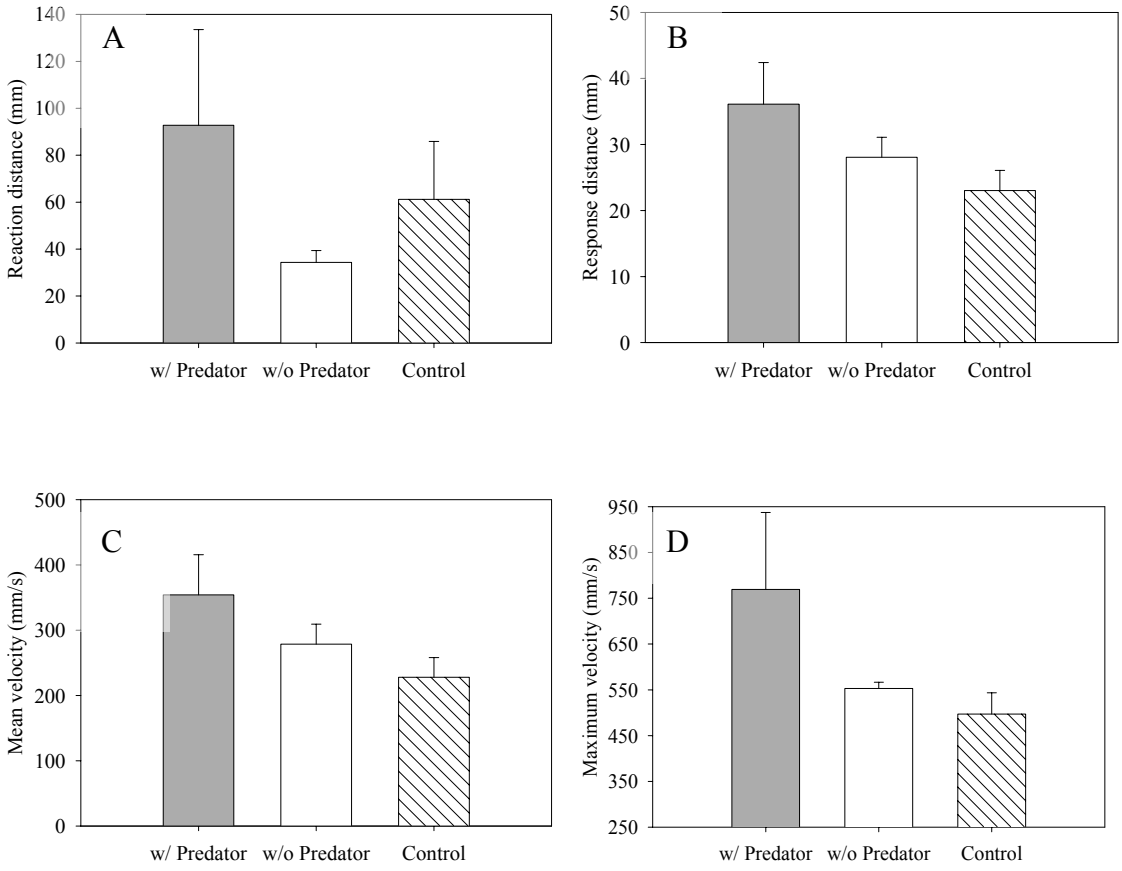

Figure 7. Mean (± S.E.) for anti-predator performance variables in red drum: (A) reaction distance, (B) response distance, (C) mean velocity, and (D) maximum velocity. Treatments = ■, with predator; □, without predator; ⧅, control.

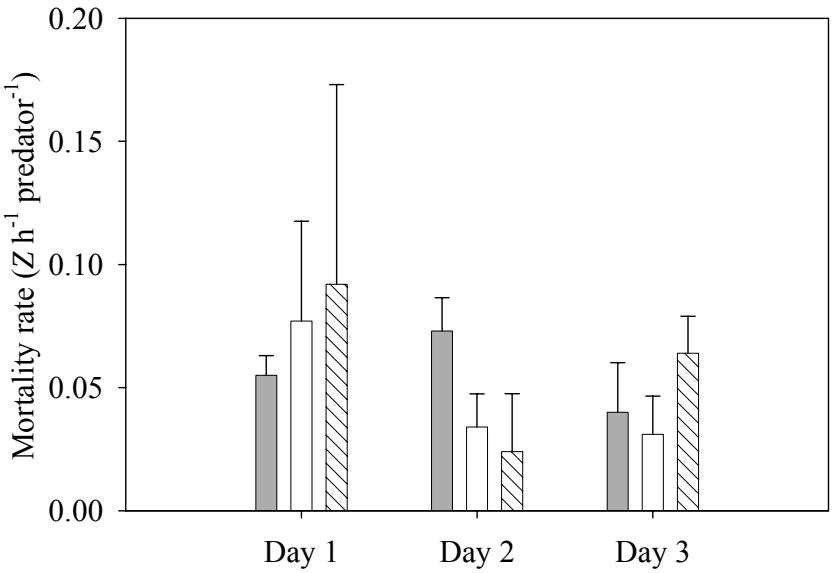

Figure 8. Comparison of instantaneous hourly mortality (*Z*) of hatchery red drum exposed to pinfish predators across days. Bars represent mean (± S.E.) for red drum with predator (■), without predator (□), and control (▨) treatments.

Discussion

During prey capture, several variables were found to differ significantly among treatments (with predator, without predator, control). Red drum reared with predators attacked mysid shrimp from a further distance compared to individuals reared without predators. Greater attack distance may lower the probability that prey may detect an approaching predator (Hunter 1972; Heath 1993; MacKenzie and Kiørboe 2000), possibly enhancing capture success. The ability to attack from a further distance would be especially beneficial when feeding on more elusive prey types, such as copepods, since these zooplankters possess a large number of mechanoreceptors (Kerfoot et al. 1980). Gape cycle duration was also found to be significantly greater for red drum from control tanks versus those reared without predators. It has been suggested that a longer gape cycle may negatively impact feeding performance by increasing the prey's chances of escape (Wintzer and Motta 2005); however, this did not appear to influence prey-capture ability in red drum as feeding attempts were ≥ 95% across all treatments. Although not significant, overall trends indicated that mean attack velocity, capture time, and gape cycle duration were all greater in red drum reared with versus without predators. This suggested that red drum reared with predators approached prey more quickly, yet took longer to acquire prey during feeding attempts.

Numerous studies have demonstrated that exposure to live predators improves anti-predator behaviors in naïve fish (Järvi and Uglem 1993; Malavasi et al. 2004). For example, Nødtvedt et al. (1999) reported that 'predator-trained' cod (*Gadus morhua*) maintained longer distances to a predator than 'predator-naïve' individuals, while Dill (1974) documented that escape velocity of the zebra danio (*Danio rerio*) increased significantly in naïve fish following exposure to predatory stimuli. In this study, exposing hatchery red drum to predators resulted in a 300% increase in reaction distance and 20 – 30% increase in response distance, mean velocity, and maximum velocity relative to individuals receiving no predator exposure. Greater distances and velocities during anti-predator responses have been shown to increase the chances of surviving a predation strike in the guppy, *Poecilia reticulata* (Walker et al. 2005). Likewise,

Fuiman et al. (2006) also demonstrated that greater reactive distance and swimming speeds are linked to escape potential in red drum. In light of the increased magnitude of anti-predator performance variables for red drum reared with versus without predators, it should be noted that no significant differences were found between treatment groups ($P > 0.05$). Closer analysis of the data indicated that anti-predator variables were 40 – 50% lower for individuals within one of the 'with predator' tanks compared to the other two tanks. When this tank was removed, statistical analysis revealed that response distance ($P = 0.046$), and maximum velocity ($P = 0.009$) were significantly greater in red drum reared with predators. Mean velocity was also close to alpha value of 0.05 ($P = 0.053$). Thus, it appears that the lack of significant findings were largely a result of poorly performing individuals from a single tank.

Behavioral studies are often confounded by high amounts of variability among individuals (Kolok et al. 1998; Gregory and Wood 1998) as well as populations (Nicoletto and Kodric-Brown 1999; Pon et al. 2007). Here, the level of inter-individual variability (CV) for red drum within each tank was high, ranging from 3.8 – 98.9% and 3.3 – 88.8% for prey-capture and anti-predator variables, respectively (Table 5). These values are much higher than that reported for other species such as coho salmon, *Oncorhynchus kisutch* (9.5 – 16.6%, Taylor and McPhail 1985), yellow perch, *Perca flavescens* (9.7 – 15.6%, Nelson 1989), and Atlantic cod, *Gadus morhua* (9.9 – 35.4%, Reidy et al. 2000). Intra-cohort variability in performance has been documented for larval red drum (Fuiman et al. 2005). Still, the fact that red drum were spawned from multiple breeding pairs in the hatchery likely increased the amount of variability witnessed in this study. These elevated CV values may have also contributed to the low power ($ß < 0.300$) associated with statistical tests, thus the lack of significant findings in the present study is likely linked to high variability (low power). Subsequent power analysis indicated that sample size should be increased from three to approximately six to eight individuals per tank in order to statistically detect a difference among treatment groups for each variable at $\alpha = 0.05$ ($ß \geq 0.800$). Alternatively, increasing the number of tank replicates may also improve the power of statistical tests.

Average mortality rates (Z $h^{-1} \cdot predator^{-1}$) for juvenile hatchery red drum were approximately 3-4x lower than previously reported values for red drum larvae (Z = 0.192, 3.6 – 6.9 mm, Fuiman 1994) and early juveniles (Z = 0.193, 10.7 – 20.9 mm, Rooker et al. 1998). Evidence suggests that responsiveness to predatory stimuli increases with ontogeny in red drum (Fuiman 1994) and other species such as herring, *Clupea harengus* (Blaxter and Fuiman 1990). Moreover, the vulnerability of red drum to piscivores has been shown to decrease substantially when individuals exceed 20 mm in total length (Fuiman 1994). Thus, the larger sizes of red drum in this study (25-30 mm) likely had an influence on the amount of predation within each tank, resulting in lower Z rates compared to previous predation trials for this species. However, physical differences between this study and others (container volume, De Lafontaine and Leggett 1988; Cowan and Houde 1993; temperature, Elliott and Leggett 1996; Elliott and Leggett 1997) may have also impacted the degree of mortality experienced by red drum, and therefore cannot be ruled out as possible sources of variability. Interestingly, a high level of variability in Z was detected among tank replicates as well as among days, possibly contributing to the lack of significant findings for mortality experiments. For example, during the first mortality experiment 20, 5, and 0 red drum were consumed from the three control tanks, while similar trends were also repeated among with and without predator tanks. Likewise, Rooker et al. (1998) and Fuiman (1994) also documented variability for red drum mortality rates among replicates when using pinfish predators, suggesting that predator motivation may vary substantially within this species.

This study indicated that predator exposure impacts survival skills linked to prey-capture and anti-predator performance in hatchery red drum. Experimental evidence has shown that even a single exposure to predatory stimuli enhanced survival behaviors in naïve fathead minnows, *Pimephales promelas* (Gazdewich and Chivers 2002), while repeated exposure events were needed to produce similar responses in Arctic charr, *Salvelinus alpinus* (Vilhunen 2006). Thus the timing and duration of exposure needed for naïve individuals to learn to avoid predators may vary among species. In some cases, the use of chemical cues, either alone (Brown and Smith 1998; Mirza and Chivers 2001)

or in combination with visual stimuli (Chivers and Smith 1994a, b; Wisenden, et al. 2004), are necessary to train naïve fish to respond to predators similar to that of their wild counterparts. Here, the use of live predators allowed red drum to be subjected to a variety of cues (e.g., visual, chemical, and mechanosensory) during exposure periods, all of which have been shown to be important in the development of predator detection and avoidance behaviors. Although there are ethical concerns with using live predators (Huntingford 1984), such methods may provide the necessary stimuli in order to properly train naïve individuals for subsequent predator-prey encounters. Currently, no pre-release exposure protocol exists for red drum; however, findings of this study suggest that even short exposure durations (1 h per day for 5 days) can influence survival behaviors, i.e., greater distances and velocities, of naïve hatchery individuals. While these results are encouraging, future studies should investigate whether longer exposure periods and/or the use of alternate predators may lead to further enhancements in the survival behaviors of hatchery red drum.

CHAPTER V

THE INFLUENCE OF DIET ON THE PERFORMANCE AND FORAGING BEHAVIOR OF HATCHERY RED DRUM

Introduction

The success of any stock enhancement program is contingent upon the survival of its hatchery-reared progeny. Nevertheless, hatchery fish often experience high levels of mortality shortly following release into the wild (Suboski and Templeton 1989; Brown and Day 2002), resulting in poor returns of stocked individuals (McNeil 1991). Experimental evidence has shown that starvation is a major contributor to mortality in hatchery fishes (Paszkowski and Olla 1985). This may result from the hatchery feeding regime, where individuals are typically reared on artificial (pellet) diets in the hatchery and are therefore largely inexperienced in capturing live prey. As a result, hatchery fish may have difficulty switching to live prey upon release (Sosiak et al. 1979; Nordeide and Salvanes 1991), leading to reduced foraging ability and poor growth and survival relative to their wild counterparts (Gillen et al. 1981; Bachman 1984; Sundström and Johnsson 2001).

The influence of diet on the behavior and post-release survival of hatchery fishes has been well documented for salmonids (Sosiak et al. 1979; Nordeide and Salvanes 1991; Maynard et al. 1996). However, information regarding the impact of diet on other species that are the focus of similar enhancement efforts, such as the red drum (*Sciaenops ocellatus*) is limited. Red drum is a heavily targeted recreational species in the U.S. and several red drum hatcheries currently exist along the Gulf of Mexico and Atlantic coasts (Woodward 2000; Smith et al. 2001). Supplemental pellet diets may be used when culturing red drum for stocking purposes (Davis 1990; Colura et al. 1991), yet the impact of these diets on the survival success of red drum is relatively unknown. In this study, hatchery red drum were reared on a diet of pellets or live prey for a pre-determined period after which the survival skills (i.e., prey-capture and anti-predator

performance) of these individuals was examined. Additionally, red drum were stocked into field mesocosms to determine whether diet received during the latter period of the hatchery grow out period (18-30 days post hatch) influenced foraging behaviors (i.e., number and type of prey consumed) of hatchery individuals in the wild.

Methods

Collection and rearing of hatchery red drum. – Red drum were obtained from the Texas Parks and Wildlife Department's (TPWD) SeaCenter hatchery (SCT) in Lake Jackson, Texas on 8 August 2005. Red drum at SCT were progeny of captive broodstock (2-3 females and 2-3 males per tank, 8 tanks), which were induced to spawn using artificial temperature and photoperiod regimes. Fertilized eggs were collected and reared in 400-l tanks until three days post hatch (dph), when they were transferred to a single 2-acre polyethylene lined pond containing copepods, nauplii and rotifers. Ponds were supplemented with 3 lbs of pellet feed (#0 crumble, Nelson and Sons, Inc.) daily when red drum reached 12 dph. When red drum were 17 dph (~12 mm standard length, SL), approximately 600 larvae were collected using a dip net and transported to a wet lab in Galveston, Texas. These fish were held overnight in fiberglass tanks (1.5 m diameter, 0.75 m deep) containing sand-filtered water (26.5-29.2^{o}C, 30-32 ppt) pumped from the Gulf of Mexico.

Red drum were stocked into eight tanks at a density of 60 fish per tank, representing pellet or live prey treatments (2 treatments x 4 replicates = 8 tanks). Red drum were reared on the two diets for a 14 d period at the end of which time individuals were 25-30 mm SL, coinciding with current TPWD release sizes (Robert R. Vega, TPWD, personal communication). Individuals from the live prey treatment were given 1- and 2-day old *Artemia franciscana* enriched with Algamac 2000 (www.algamac.com). Mysid shrimp (Mysidacea sp., < 4 mm total length) collected from a nearby estuary were also added to the tanks for the final 10 days of the rearing process. Red drum from the pellet treatment were given 4-6 g of 400-700 µ pellet feed

(Otohime B1, B2, and Rangen #1) throughout the entire rearing period, consistent with the feeding protocol outlined for red drum by Holt (1993).

High-speed video trials. – After the rearing process was completed, three red drum (n = 3) were randomly chosen from each tank for use in high-speed filming trials. Individuals were placed into separate chambers (18 cm x 10 cm), and prey-capture and anti-predator performance was recorded for each fish at 250 frames per second (fps) using a high-speed video camera (Redlake MotionScope PCI 1000S). A 1-cm x 1-cm grid placed behind the fish was used to provide scale during all filming events. Each event was referenced to time zero, corresponding to the frame prior to mouth opening during feeding, and the frame immediately preceding the first movement of the fish during an anti-predator response.

Prey-capture performance was evaluated by filming individual red drum feeding on mysid shrimp, a natural prey item for red drum larvae and juveniles (Soto et al. 1998). Several mysid shrimp were released into the chamber and feeding events were recorded until red drum became satiated. Only those feeding events that occurred laterally to the camera were used in the final analysis and four variables were recorded for each prey-capture event: (1) attack distance, distance from the tip of the premaxilla to the closest point on the prey at the beginning of prey capture (mm), (2) mean attack velocity, average red drum velocity from time zero to when prey completely entered the mouth (mm/s), (3) capture time, time to when prey completely entered the mouth (ms), and (4) gape cycle duration, time elapsed from time zero to when mouth closes (ms).

Following feeding trials, individuals were moved to a separate control box to record anti-predator performance. Anti-predator performance was elicited by releasing a visual stimulus consisting of a 4.5-cm diameter bulls-eye target on a swinging pendulum arm. This stimulus was modeled after Batty (1989) and has been shown to produce anti-predator behaviors in red drum larvae and juveniles (Fuiman and Cowan 2003; Smith and Fuiman 2004). Anti-predator sequences were filmed from above and began when the red drum was near the front of the container and facing less than 90º toward the direction of the stimulus. When the subject was in position, the pendulum was released,

sending the target toward the container. Four variables were recorded for each anti-predator event: (1) reaction distance, distance between red drum and center of target at time zero (mm), (2) response distance, distance traveled during the first 100 ms of response (mm), (3) maximum velocity, maximum velocity reached during response (mm/s), and (4) maximum acceleration, maximum acceleration reached during a response (mm/s^2). Only the first 100 ms of each anti-predator event was analyzed since fish often made contact with the sides of the chamber or swam out of the field of view after this time. Each individual was given 15-20 min between successive events in order to allow for recovery and to prevent habituation to the stimulus. At the completion of filming trials, red drum were anesthetized with tricaine methanesulfonate (MS-222) and measured to the nearest 0.1 mm.

On average, three prey-capture and three anti-predator events were recorded for each red drum. Video footages were analyzed at 2-4x magnification using Redlake MotionScope 2.30.0 and Peak Motus 8.0 software. Displacement data were generated by tracking a digitized point on the center of the eye during prey capture, and on the center of mass (~30% from tip of snout, verified from preserved specimens) during anti-predator events. Using QuickSAND (Walker 1997), a generalized cross-validatory (GCV) quintic spline algorithm was applied to estimate velocity and acceleration. This algorithm was used since it has been shown to provide an accurate estimate of velocity and acceleration rates at the frame rate (250 fps) and magnification (2-4x) specified in this study (Walker 1998).

Field mesocosm experiment. – Red drum reared on the two diets for 14 d were stocked into eight separate 1-m diameter fiberglass mesocosms located in Galveston Bay, Texas, to test whether exposure to the two diets in the laboratory translated into foraging differences in the field (four mesocosms per treatment, 50 fish per tank). The bottom of each mesocosm was open and four 6-$inch^2$ mesh panels were located around the base. At 1, 3, and 5 days post-stocking, five red drum (n = 5) were randomly sampled from each mesocosm and immediately placed on dry ice. Sampling occurred at

similar times in the early afternoon (approximately 1300 h), coinciding with the diurnal feeding habitats described for this species (Holt and Holt 2000).

In the laboratory, stomachs were removed from each fish and preserved in 10% formalin. Stomach contents were sorted, counted and identified to general taxonomic categories (e.g., copepods, polychaetes, shrimp) using a dissecting microscope. The presence of empty stomachs was noted for red drum reared on either diet. Material which could not be properly identified to a particular prey category was designated as 'unknown prey', while detritus (e.g., sand, stones, plant material) was designated as a separate category. Contents were oven-dried separately by category at 140^{o} F (60^{o} C) for 24 hours (Hyslop 1980) and then weighed to the nearest 0.00001 g.

Data analysis. – All data were tested for normality and homogeneity of variances using Kolmogorov-Smirnov and Levene's tests, respectively. Three variables (attack distance, capture time and gape cycle duration) were Ln-transformed in order to meet the assumptions of parametric statistics. Values for prey-capture and anti-predator variables were regressed against the length for each individual to correct for any size-related differences, and the size-removed residuals were used in all further analyses. Differences in prey-capture and anti-predator performance variables between diets were tested using repeated-measures analysis of variance (ANOVA), since individuals from the same tank were not truly independent measures. Additionally, separate univariate contrasts were conducted on tank means (i.e. average response of three red drum in each tank) for each prey-capture and anti-predator performance variable. Results of univariate contrasts for tank mean data were identical to that of repeated-measures ANOVA for the performance variables measured, therefore only repeated-measures findings are presented.

Three dietary measures were used to describe differences in prey selectivity between diets, including: percent frequency of occurrence (%F), percent numerical abundance (%N), and percent dry weight (%W). All three measures were performed on pooled stomach contents for each sampling day; however, contents were pooled across all three days to describe overall differences based upon diet (i.e., pellet or live prey) (5

fish x 4 treatments x 3 days; n = 60 per diet treatment). Unknown prey and detritus categories were not included in the calculation for percent numerical abundance; however, they were included in calculations for percent frequency of occurrence (%F) and percent dry weight (%W). The index of relative importance, IRI = (%N + %W) · (%F), was used to provide a measure of the dietary importance of each prey category (Hyslop 1980). Additionally, hierarchical cluster analysis (CLA) was performed using the Bray-Curtis similarity index and pooled percent dry weight (%W) values for each day (PRIMER 5.0), thus allowing us to group fish sampled on the three days (1, 3 and 5) according to foraging behavior. All other statistics were conducted using SPSS 13.0 and $\alpha = 0.05$.

Results

At the beginning of rearing trials, mean (± S.E.) lengths of red drum were 12.4 ± 0.3 and 12.5 ± 0.4 mm for pellet and live prey treatments, respectively. After the 14 d rearing period, mean (± S.E.) lengths were slightly lower for red drum reared on pellets versus live prey (26.1 ± 0.9 mm versus 28.1 ± 0.9 mm); however, these differences were not found to be statistically significant ($P = 0.147$, power = 0.301). Additionally, growth rates (± S.E.) were comparable over the 14 d period at 1.0 ± 0.1 mm/d for red drum reared on pellets and 1.1 ± 0.1 mm/d for red drum reared live prey.

Prey-capture performance. – Red drum prey-capture attempts resulted in successful acquisition of a prey item ~90% of the time for fish reared on both pellets and live prey. Repeated-measures ANOVA indicated that red drum reared on pellets had significantly longer gape cycle duration than individuals reared on live prey ($F = 6.856$, df = 1, 6, $P = 0.040$) (Figure 9). Although not statistically significant, attack distance ($P = 0.562$, power = 0.082) as well as capture time ($P = 0.417$, power = 0.115) were higher for red drum reared on pellets (Figure 9A, C), while the reverse was true for mean attack velocity ($P = 0.620$, power = 0.073) (Figure 9B).

Anti-predator performance. – Repeated-measures ANOVA indicated that red drum reared on live prey exhibited greater maximum velocity ($F = 12.572$, df = 1, 6, $P =$

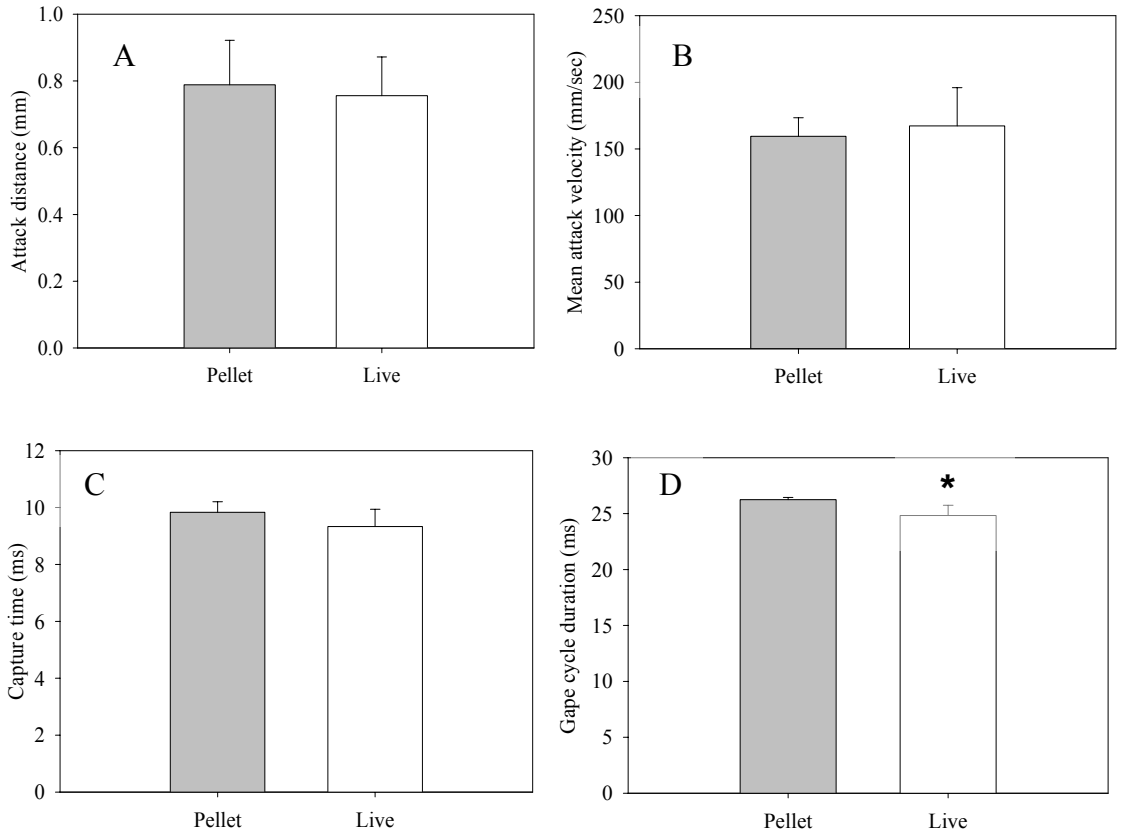

Figure 9. Mean (± S.E.) for variables associated with prey-capture performance in red drum: (A) attack distance, (B) mean attack velocity, (C) capture time, and (D) gape cycle duration. Shaded bars (■) designate fish reared on pellets, and open bars (□) designate fish reared on live prey (*$P < 0.05$).

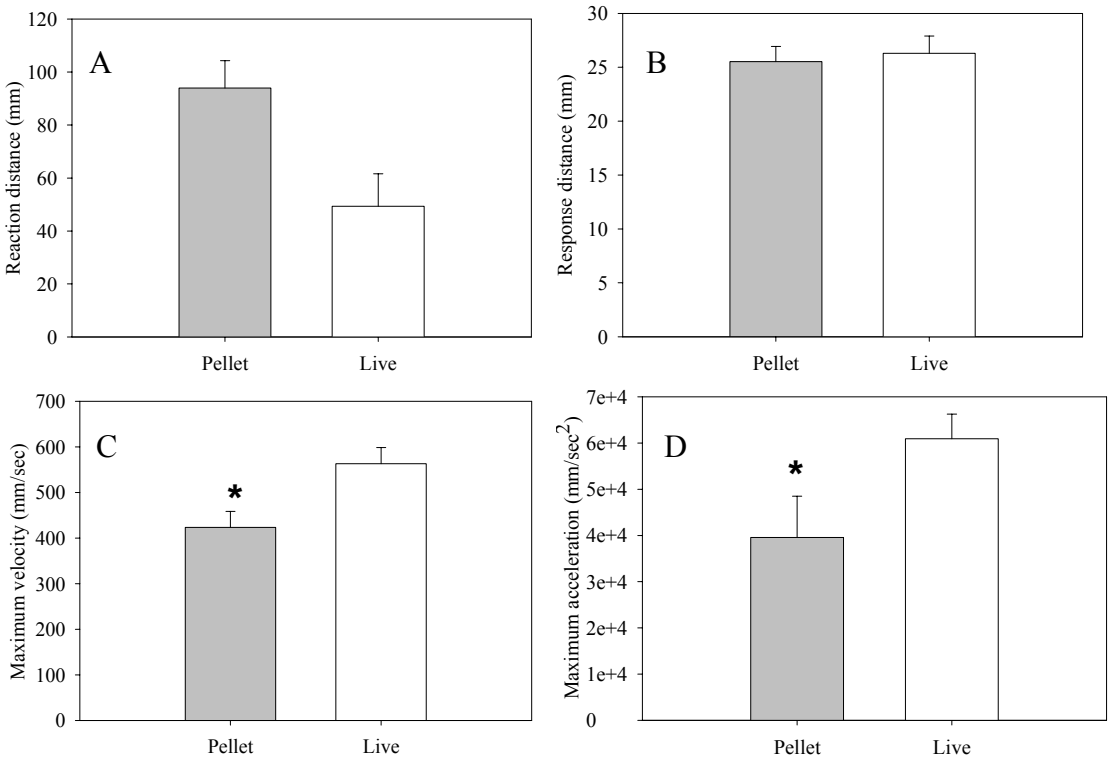

Figure 10. Mean (± S.E.) for variables associated with anti-predator performance in red drum: (A) reaction distance, (B) response distance, (C) maximum velocity, and (D) maximum acceleration. Shaded bars (■) designate fish reared on pellets, and open bars (□) designate fish reared on live prey (*$P < 0.05$).

0.012) and maximum acceleration (F = 8.422, df = 1, 6, *P* = 0.027) compared to individuals reared on pellets (Figure 10). During anti-predator events, maximum velocity (mean ± S.E.) for red drum reared on live prey was 562 ± 35 versus 423 ± 35 mm/s for individuals reared on pellets, while maximum acceleration was 60,932 ± 5,325 versus 39,564 ± 8,926 mm/s^2, respectively. Reaction distance (*P* = 0.057, power = 0.503) (Figure 10A) and response distance (*P* = 0.587, power = 0.078) (Figure 10B) did not differ significantly between red drum reared on the two diets.

Field mesocosm experiment. – Nine prey types were identified in the stomachs of red drum reared on pellets, while eight prey types were found for individuals reared on live prey (Table 6). Overall, a higher percentage of red drum reared on pellets had empty stomachs (20.0%) versus individuals reared on live prey (11.7%). Analysis of stomach contents (pooled across days) revealed that for red drum reared on pellets, copepods were the most common prey type based upon frequency of occurrence (77.6%), numerical abundance (76.5%), and prey weight (35.4%) (Table 6). Similarly, copepods were the most common prey type for red drum reared on live prey based upon frequency of occurrence (54.7%) and numerical abundance (92.9%). Shrimp were more important in regards to percent dry weight (38.6%) for red drum reared on live prey; however, frequency of occurrence and numerical abundance were < 2% for this prey type. Estimates of IRI indicated that copepods were the most important prey type consumed by red drum on both diets, followed by oligochaetes and polychaetes for individuals reared on pellets, and shrimp and oligochaetes for fish reared on live prey (Table 6). Although some prey types were consumed by red drum reared on both diets (e.g., copepods, oligochaetes, polychaetes), several prey types were exclusive to individuals reared on pellets or live prey, albeit percent frequency of occurrence was low for these prey types. For example, red drum reared on pellets consumed gastropods, zoea, nauplii, and isopods, while these prey types were absent in fish reared on live prey (Table 6). Likewise, shrimps, fishes, and amphipods were consumed by red drum reared on live prey, but not those reared on pellets (Table 6). Cluster analysis performed on daily pooled dry weights (%W) indicated that red drum reared on pellets and live prey

Table 6. Composition of red drum stomach contents expressed as percent frequency of occurrence (%F), percent numerical abundance (%N), percent dry weight (%W), and index of relative importance [IRI = (%N + %W) · (%F)]. Values represent pooled stomach contents across all sampling days.

Prey-type treatment	Pellet				Live			
Prey category	%F	%N	%W	IRI	%F	%N	%W	IRI
Copepoda	77.6	76.5	35.4	8677.9	54.7	92.7	12.7	5770.3
Oligochaeta	18.4	5.5	10.3	289.5	11.3	2.6	0.6	35.9
Polychaeta	10.2	14.5	1.9	167.2	1.9	0.7	5.4	11.5
Shrimp sp.	--	--	--	--	1.9	0.7	38.6	74.3
Gastropoda	2.0	0.5	10.3	21.9	--	--	--	--
Zoea	4.1	1.5	0.7	8.9	--	--	--	--
Osteichthys	--	--	--	--	1.9	2.9	0.6	6.7
Nauplii	4.1	1.0	0.5	5.9	--	--	--	--
Isopoda	2.0	0.5	1.5	4.0	--	--	--	--
Amphipoda	--	--	--	--	1.9	0.4	0.1	0.8
Unknown prey	67.4	N/A	36.6	N/A	100.0	N/A	41.1	N/A
Detritus	8.2	N/A	2.9	N/A	3.8	N/A	0.9	N/A

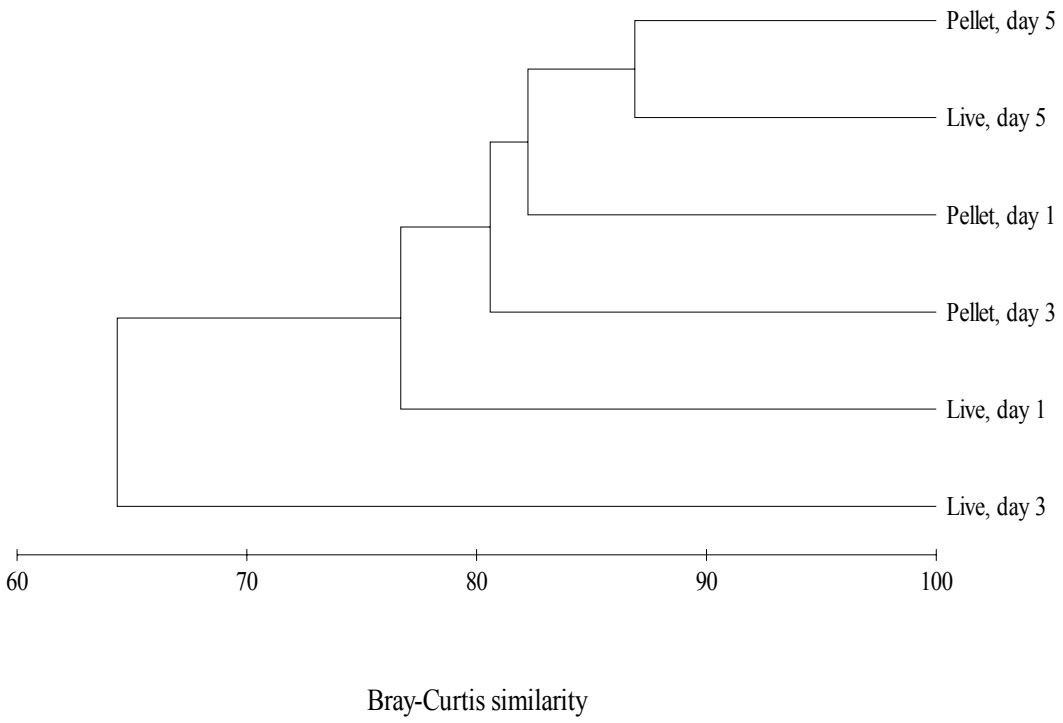

Figure 11. Heirarchical cluster analysis based on percent dry weight of each prey category (%W) for fish reared on pellet or live prey diets at 1, 3, and 5 days post-stocking.

grouped together after 5 days post-stocking, indicating that foraging behaviors became more similar over time (Figure 11).

Discussion

Findings of the present study indicated that prey-capture performance of hatchery red drum differed between fish reared on the two diets. During feeding events, red drum reared on live prey demonstrated significantly faster gape cycle duration (~24 ms) compared to fish reared on pellets (~26 ms). Although this did not appear to impact capture rates in this study, more rapid feeding bouts by fish reared on live prey may enhance capture probability in the wild by reducing the amount of time for prey to escape (Wintzer and Motta 2005). This behavior would be especially beneficial when targeting more elusive prey types such as fish, shrimp and copepods, all of which are important prey items for red drum larvae and juveniles (Bass and Avault 1975; Peters and McMichael 1987; Soto et al. 1998). Interestingly, all other prey-capture performance variables (attack distance, mean attack velocity, and capture time) remained similar between red drum reared on the two diets. It is possible that the presence of live prey in TPWD ponds in the weeks prior to collection may have mitigated some of the negative effects of rearing with pellets, thereby reducing the magnitude of diet-induced differences in this study.

Anti-predator performance of hatchery red drum also differed between individuals reared on the two diets. Specifically, maximum velocity and maximum acceleration values were approximately 25% greater for red drum reared on live prey versus individuals reared on pellets. The ability of fish to achieve high velocity and acceleration during escape reactions is critical to determining the outcome of predator-prey encounters (Webb 1976; Weihs and Webb 1984; Domenici and Blake 1991). For example, Walker et al. (2005) demonstrated that greater maximum velocity and maximum acceleration values contributed to faster starts in the guppy (*Poecilia reticulata*) leading to a 2.3-fold increase in the odds of surviving strikes by pike cichlid predators (*Crenicichla alta*). Greater velocities and accelerations during escape events

for hatchery red drum reared on live prey could also reduce capture probability for these individuals, assuming that the behaviors witnessed during filming trials are comparable to that of actual predator-prey encounters. The use of pellet feeds has been linked to increased fat levels (Kucska et al. 2006) and reduced swimming stamina (Vincent 1960; Green 1964; Thorstad et al. 1997) in hatchery fishes, thus fish reared on pellets may have been in poorer condition than fish reared on live prey (see Davis and Olla 1992; De Silva et al. 2002). Alternatively, aspects of the live prey diet, e.g., increased activity associated with pursuit and capture of moving prey, may have enhanced swimming ability in hatchery red drum reared on live prey, leading to improved swimming performance in these individuals relative to fish reared on pellets. Although further experiments are necessary in order to determine the exact reason(s) for these differences, evidence from this study suggests that experience with live prey enhances certain anti-predator behaviors in hatchery red drum.

Diet also appeared to influence the foraging behaviors of hatchery red drum under field conditions. For example, the proportion of empty stomachs found in red drum reared on pellets was approximately 2x higher than fish reared on live prey. The higher percentage of empty stomachs for red drum reared on pellets is in line with previous evidence showing that naïve hatchery fish often have difficulty switching to natural prey (Sosiak et al. 1979; Nordeide and Salvanes 1991), and suggests that these fish may suffer higher rates of starvation after release relative to individuals from the live prey treatment. Additionally, starving fish could be more prone to predation pressures, since they may be too weak to respond to predatory threat or may develop maladaptive behaviors (i.e., swimming off the bottom) (Furuta 1996; Hossain et al. 2002), thus placing them at greater risk for predation. In laboratory trials, Hossain et al. (2002) demonstrated that the average mortality rate of starved Japanese flounder (*Paralichthys olivaceus*) was twice that of fed fish; however, the level of predation experienced by starving hatchery fish may be much greater in the wild, especially when prey resources are limited.

Overall, three major prey categories (copepods, oligochaetes, polychaetes) were consumed by hatchery red drum reared on pellet and live prey diets. Still, several prey types were exclusive to red drum reared on either diet, indicating that some degree of selectivity occurred during field trials. Differences in prey selection may be linked to the development of different 'search images' during the rearing process, leading to the consumption of certain prey which were familiar in terms of size, shape and/or color to the rearing diet (Ware 1971; Lawrence and Allen 1983; Langley 1996). This is exemplified by the fact that hatchery fish often consume stones or other pellet-like objects (O'Grady 1983; Ellis and Nash 1998; Ellis et al. 2002) or round prey types (e.g., Glossosomatidae larvae; Ersbak and Haase 1983), as these items tend to resemble artificial pellet feeds. Such behaviors may also explain the higher frequency of occurrence of detritus as well as the consumption of gastropods by red drum reared on pellets in this study. In addition, prey mobility may have influenced selectivity in hatchery red drum. Generally speaking, red drum reared on pellets consumed higher numbers of non-elusive prey types (e.g., polychaetes, oligochaetes and gastropods) than individuals reared with live prey. Similar findings have been reported by Nordeide and Salvanes (1991) who found that hatchery cod (*Gadus morhua*) preferentially consumed slower moving prey, presumably due to their inability to capture more elusive prey types. Indeed, naïve fish have been shown to expend more energy and exhibit decreased capture success when attempting to capture faster-moving prey, although these behaviors do improve with experience (Steingrund and Fernö 1997; Wintzer and Motta 2005).

Interestingly, cluster analysis indicated that feeding behaviors of red drum reared on the two diets became more similar over time. Experimental evidence suggests that while fish reared on pellets initially demonstrate differences in the types of prey consumed compared to wild fish, these behaviors often dissipate after several days or weeks as experience is gained (Johnsen and Ugedal 1986, 1989; Munakata et al. 2000). While it is possible that similar learning effects may have impacted red drum foraging behaviors to some degree in this study, signs of starvation in fish collected after day 5 suggest that prey availability within field mesocosms was in decline, and this may have

reduced selective feeding behaviors. Selective foraging implies that predators do not take prey as it is encountered, but rather may reject certain prey items with low profitability in favor of those which provide the largest gross energy gain (Backwell et al. 1998). However, when prey densities are low, predators may be forced to shift to less profitable prey, leading to slower growth or even starvation (Hoxmeier et al. 2004). This was likely the case for red drum in this study as high red drum densities within field mesocosms may have depleted prey reserves, resulting in limited availability over the course of field trials.

In conclusion, red drum reared on live prey exhibited greater performance (e.g., faster gape cycle duration, greater maximum velocity, and maximum acceleration) and foraging ability (e.g., lower proportion of empty stomachs) relative to fish reared on pellets. Thus, exposure to live prey appears to enhance behaviors linked to survival in red drum and this is consistent with pre-release exposure studies for other hatchery fishes (Colgan et al. 1986; Maynard et al. 1996; Sundström and Johnsson 2001). Hatchery fish are often reared on artificial pellet diets, therefore feeding behaviors are often poorly developed in these individuals (Olla et al. 1998; Brown and Day 2002) and this has been linked to high levels of mortality following release. Still, evidence suggests that even brief exposure durations to live prey (ca. 10-15 exposures) may improve the prey-capture ability of hatchery progeny (Ware 1971; Reirez et al. 1998; Wintzer and Motta 2005) and therefore live prey should be introduced into the diet whenever possible. Moreover, fish reared on live prey may demonstrate the ability to generalize to other prey types and this may help to facilitate the transition from the hatchery environment to the wild (Brown et al. 2003). Since most of the mortality experienced by hatchery fishes occurs shortly after release (Olla et al. 1998), there is little opportunity to develop critical behaviors necessary for survival. Results of this study and others suggest that exposure to live prey diets while in captivity may reduce high mortality rates on hatchery progeny by enhancing both prey-capture and anti-predator performance in these fishes and this may positively impact survival success of stocked individuals.

CHAPTER VI

SUMMARY AND CONCLUSIONS

Findings of this research indicate that hatchery and wild red drum differ in terms of their survival skills, yet exposure to certain types of stimuli (e.g., predators, live prey) may enhance the behavioral performance of hatchery individuals. To my knowledge, this study is the first to demonstrate that hatchery red drum may benefit from the use of pre-release exposure techniques and provides further evidence of the importance of early life experience on the development of survival skills in captive-reared fishes.

Comparisons of the survival skills between red drum from different hatcheries and bays (i.e., wild fish) showed that prey-capture performance was relatively consistent between hatchery and wild individuals. This was likely a consequence of the presence of live prey in TPWD rearing ponds, thus leading to the development of natural feeding behaviors in hatchery red drum. In contrast, anti-predator performance variables (e.g., reaction distance, response distance, mean velocity, and maximum velocity) were greater in magnitude for hatchery versus wild red drum, although this may simply reflect the inability of hatchery fish to discriminate between threatening and non-threatening stimuli. A high amount of variability (CV) in red drum performance was witnessed among locations as well as origins (i.e., hatcheries versus bays); however, CVs were typically greatest among hatchery red drum, possibly due the lack of selective mortality in hatchery environments.

Exposure to natural habitat (*S. alterniflora* marsh) did not appear to enhance overall survival skills in hatchery red drum. Time to maximum velocity was faster for red drum reared in vegetation, yet these individuals reacted at a shorter distance to the visual stimulus and took longer to capture prey compared to fish reared without vegetation. Conversely, ontogeny had a direct influence on performance in hatchery individuals, as older fish were found to demonstrate greater distances and timings during prey-capture events. Anti-predator variables such as reaction distance and time to

maximum velocity decreased with age. Additionally, inter-individual variability (CV) was high among fish reared both with and without habitat.

Hatchery red drum exposed to pinfish (*L. rhomboides*) predators exhibited greater magnitude of response in terms of prey-capture and anti-predator performance than naïve individuals. Attack distance was significantly greater in red drum reared with predators. Red drum reared with predators also exhibited ~300% greater reaction distance and 20-30% greater response distance, mean velocity and maximum velocity during anti-predator events than fish reared without predators. Still, these differences were not statistically significant perhaps due to low power ($\beta < 0.300$) of statistical tests. In mortality experiments where free-ranging pinfish predators were used, instantaneous mortality rates (Z) varied from 0.047 – 0.060 $h^{-1} \cdot predator^{-1}$ and did not differ significantly between treatments. High levels of variability in Z were witnessed among tank replicates and this was likely due to differences in predator motivation.

Diet was shown to significantly impact the performance of hatchery red drum. Red drum reared on live prey demonstrated behaviors consistent with enhanced survival success (e.g., faster gape cycle, greater maximum velocity and maximum acceleration) compared to individuals reared on pellets. In field mesocosm experiments, hatchery red drum reared on live prey exhibited lower proportion of empty stomachs versus pellet-reared individuals. Red drum reared on both diets demonstrated some degree of prey selectivity during field experiments but it is unknown whether this occurred due to the development of different 'search images' or preference for slower-moving prey types by individuals reared on pellets. Interestingly, foraging behaviors became more similar for fish reared on the two diets over time, but it is unclear whether this was due to learning effects or simply a consequence of reduced prey availability within mesocosms.

Stock enhancement of hatchery red drum in Texas has been conducted for over 20 years, but there is little information on the behavioral performance of these individuals. Here, I present findings which show that hatchery red drum differ in terms of certain survival behaviors from their wild counterparts, but that such differences can be mediated through the use of various pre-release exposure techniques. For TPWD

fish, aspects of the current rearing protocol (e.g., use of live prey in ponds) may help to prepare individuals for survival following release; however, results of this research indicate that the incorporation of alternate stimuli (e.g., predators) may further enhance survival success in these individuals. Future studies should investigate whether hatchery fish could benefit from a combination of natural stimuli (e.g., habitat and live prey) or the use of 'trained' conspecifics in the rearing environment. It is also imperative to conduct follow-up studies in the field in order to determine if pre-release exposure received during the rearing process constitutes increased survival in the wild.

REFERENCES

Álvarez D., and A. Nicieza. 2003. Predator avoidance behaviour in wild and hatchery-reared brown trout: the role of experience and domestication. Journal of Fish Biology 63:1565-1577.

Bachman, R.A. 1984. Foraging behavior of free-ranging wild and hatchery brown trout in a stream. Transactions of the American Fisheries Society 113:1-32.

Backwell, P.R.Y., P.D. O'Hara, and J.H. Christy. 1998. Prey availability and selective foraging in shorebirds. Animal Behavior 55:1659-1667.

Baltz D.M., D. Rakocinski, and J.W. Fleeger. 1993. Microhabitat use by marsh-edge fishes in a Louisiana estuary. Environmental Biology of Fishes 36:109-126.

Basaran, F., H. Ozbilgin, and Y.D. Ozbilgin. 2007. Comparison of the swimming performance of farmed and wild gilthead sea bream, *Sparus aurata*. Aquaculture Research 38:452-456.

Bass, R.J., and J.W. Avault, Jr. 1975. Food habits, length-weight relationship, condition factor, and growth of juvenile red drum, *Sciaenops ocellata*, in Louisiana. Transactions of the American Fisheries Society 104:3545.

Batty, R.S. 1989. Escape responses of herring larvae to visual stimuli. Journal of the Marine Biological Association of the United Kingdom 69(3):647-654.

Beck, J.L., and R.G. Turingan. 2007. The effects of zooplankton swimming behavior on prey-capture kinematics of red drum larvae, *Sciaenops ocellatus*. Marine Biology 151(4):1463-1470.

Bennett, A.F., T. Garland, Jr., and P.L. Else. 1989. Individual correlation of morphology, muscle mechanics, and locomotion in a salamander. American Journal of Physiology 256:R1200-1208.

Berejikian, B.A., E.P. Tezak, T.A. Flagg, A.L. LaRae, E. Kummerow, and C.V.W. Mahnken. 2000. Social dominance, growth, and habitat use of age-0 steelhead (*Oncorhynchus mykiss*) grown in enriched and conventional hatchery rearing environments. Canadian Journal of Fisheries and Aquatic Sciences 57:628-636.

Berejikian, B.A., E.P. Tezak, S.C. Riley, and A.L. LaRae. 2001. Competitive ability and social behaviour of juvenile steelhead reared in enriched and conventional hatchery tanks and a stream environment. Journal of Fish Biology 59:1600-1613.

Bergman, P., and D.J. Irschick. 2006. Effects of temperature on maximum acceleration, deceleration and power output during vertical running in geckos. The Journal of Experimental Biology 209:1404-1412.

Björnsson, B. 1993. Swimming speed and swimming metabolism of Atlantic cod (*Gadus morhua*) in relation to available food: a laboratory study. Canadian Journal of Fisheries and Aquatic Sciences 50:2542-2551.

Blankenship, H.L., and K.M. Leber. 1995. A responsible approach to marine stock enhancement. American Fisheries Society Symposium 15:167-175.

Blaxter, J.H.S., and L.A. Fuiman. 1990. The role of the sensory systems of herring larvae in evading predatory fishes. Journal of the Marine Biological Association of the United Kingdom 70:413-427.

Bowles, E.C. 1995. Supplementation: panacea or curse for the recovery of declining fish stocks? American Fisheries Society Symposium 15:277-283.

Braithwaite, V.A., and A.G.V. Salvanes. 2005. Environmental variability in the early rearing environment generates behaviourally flexible cod: implications for rehabilitating wild populations. Proceedings of the Royal Society B 272:1107-1113.

Breck, J.E., and M.J. Gitter. 1983. Effect of fish size on the reactive distance of bluegill (*Lepomis macrochirus*) sunfish. Canadian Journal of Fisheries and Aquatic Sciences 40:162-167.

Brennan, N.P., K.M. Leber, and B.R. Blackburn. 2007. Use of coded-wire and visible implant elastomer tags for marine stock enhancement with juvenile red snapper *Lutjanus campechanus*. Fisheries Research 83:90-37.

Brown, C., and K. Warburton. 1999. Social mechanisms enhance escape responses in shoals of rainbowfish, *Melanotaenia duboulayi*. Environmental Biology of Fishes 56:455-459.

Brown, C., and K. Laland. 2001. Social learning and life skills training for hatchery reared fish. Journal of Fish Biology 59:471-493.

Brown, C., and R. Day. 2002. The future of stock enhancements: bridging the gap between hatchery practice and conservation biology. Fish and Fisheries 3:79-94.

Brown, C., T. Davidson, and K. Laland. 2003. Environmental enrichment and prior experience of live prey improve foraging behaviors in hatchery-reared Atlantic salmon. Journal of Fish Biology 63(Supplement A):187-196.

Brown, G.E., and R.J.F. Smith. 1998. Acquired predator recognition in juvenile rainbow trout (*Oncorhynchus mykiss*): conditioning hatchery-reared fish to recognize chemical cues of a predator. Canadian Journal of Fisheries and Aquatic Sciences 55:611-617.

Chivers, D.P., and R.J.F. Smith. 1994a. Fathead minnows, *Pimephales promelas*, acquired predator recognition when alarm substance is associated with the sight of unfamiliar fish. Animal Behaviour 48:597-605.

Chivers, D.P., and R.J.F. Smith. 1994b. The role of experience and chemical alarm signaling in predator recognition by fathead minnows, *Pimephales promelas*. Journal of Fish Biology 44:273-285.

Colgan, P.W., J.A. Brown, and S.D. Orsatti. 1986. Role of diet and experience in the development of feeding behaviour in largemouth bass, *Micropterus salmoides*. Journal of Fish Biology 28:161-170.

Colura, R.L., A. Henderson-Arzapalo, and A.F. Maciorowski. 1991. Culture of red drum. Pages 149-166 *in* J.P. McVey, editor. Handbook of Mariculture, Volume II Finfish Aquaculture. CRC Press, Boca Raton, Florida, United States.

Conover, D.O. 1998. Local adaptation in marine fishes: evidence and implications for stock enhancement. Bulletin of Marine Science 62(2):477-493.

Cook, A. 1996. Ontogeny of feeding morphology and kinematics in juvenile fishes: a case study of the cottid fish *Clinocottus analis*. The Journal of Experimental Biology 199:1961-1971.

Cowan, J.H., and E.D. Houde. 1993. Relative predation potentials of scyphomedusae,

ctenophores and planktivorous fish on ichthyoplankton in Chesapeake Bay. Marine Ecology Progress Series 95:55-65.

Cowx, I.G. 1999. An appraisal of stocking strategies in the light of developing country constraints. Fisheries Management and Ecology 6:21-34.

Cucherousset, J., J.-M. Paillisson, and J.-M. Roussel. 2007. Using PIT technology to study the fate of hatchery-reared YOY northern pike released into shallow vegetated areas. Fisheries Research 85:159-164.

Davis, J.T. 1990. Red drum: production of food fish. Southern Regional Aquaculture Center. SRAC Publication No. 322.

Davis, M.W., and B.L. Olla. 1992. Comparison of growth, behavior and lipid concentrations of walleye pollock *Theragra chalcogramma* larvae fed lipid-enriched, lipid-deficient and field-collected prey. Marine Ecology Progress Series 90:23-30.

De Lafontaine, Y., and W.C. Leggett. 1988. Predation by jellyfish on larval fish: an experimental evaluation employing in situ enclosures. Canadian Journal of Fisheries and Aquatic Sciences 45:1173-1190.

DeSilva, S.S., R.M. Gunasekera, R.A. Collins, and B.A. Ingram. 2002. Performance of juvenile Murray cod *Maccullochella peelii peelii* (Mitchell), fed with diets of different protein to energy ratio. Aquaculture Nutrition 8:79-85.

Dill, L.M. 1974. The escape response of the zebra danio (*Brachydanio rerio*). I. The stimulus for escape. Animal Behaviour 22:710-721.

Domenici, P., and R.W. Blake. 1997. Review: the kinematics and performance of fish fast-start swimming. The Journal of Experimental Biology 200:1165-1178.

Eaton, R.C., J. Nissanov, and R. DiDomenico. 1991. The role of the Mauthner cell in sensorimotor integration by the brainstem escape network. Brain Behavior and Evolution 37:272-285.

Elliott, J.K., and W.C. Leggett. 1996. The effect of temperature on predation rates of a fish (*Gasterosteus aculeatus*) and a jellyfish (*Aurelia aurita*) on larval capelin (*Mallotus villosus*). Canadian Journal of Fisheries and Aquatic Sciences 53:1393-1402.

Elliott, J.K., and W.C. Leggett. 1997. Influence of temperature on size-dependent predation by a fish (*Gasterosteus aculeatus*) and a jellyfish (*Aurelia aurita*) on larval capelin (*Mallotus villosus*). Canadian Journal of Fisheries and Aquatic Sciences 54:2759-2766.

Ellis, T., B.R. Howell, and J. Hayes. 1997. Morphological differences between wild and hatchery-reared turbot. Journal of Fish Biology 50:1124-1128.

Ellis, T., and R.D.M. Nash. 1998. Predation on wild 0-group flatfishes by released and wild turbot, *Scophthalmus maximus*. Pages 319-326 *in* I.G. Cowx, editor. Stocking and Introduction of Fish. Springer, Oxford, United Kingdom.

Ellis, T., R.N. Hughes, and B.R. Howell. 2002. Artificial dietary regime may impair subsequent foraging behavior of hatchery-reared turbot released into the natural environment. Journal of Fish Biology 61:252-264.

Engström-Öst, J., and M. Lehtiniemi. 2004. Threat-sensitive predator avoidance by

pike larvae. Journal of Fish Biology 65:251-261.

Ersbak, K., and B.L. Haase. 1983. Nutritional deprivation after stocking as a possible mechanism leading to mortality in stream-stocked brook trout. North American Journal of Fisheries Management 3:142-151.

Fleming, I.A., B. Jonsson, and M.R. Gross. 1994. Phenotypic divergence of sea-ranched, farmed and wild salmon. Canadian Journal of Fisheries and Aquatic Sciences 51:2808-2824.

Fuiman, L.A. 1994. The interplay of ontogeny and scaling in the interactions of fish larvae and their predators. Journal of Fish Biology 45(Supplement A):55-79.

Fuiman, L.A., and J.H. Cowan. 2003. Behavior and recruitment success in fish larvae: repeatability and covariation of survival skills. Ecology 84(1):53-67.

Fuiman, L.A., J.H. Cowan, M.E. Smith, and J.P. O'Neal. 2005. Behavior and recruitment success in fish larvae: variation with growth rate and batch effect. Canadian Journal of Fisheries and Aquatic Sciences 62:1337-1349.

Fuiman, L.A., K.A. Rose, J.H. Cowan, Jr., and E.P. Smith. 2006. Survival skills required for predator evasion by fish larvae and their relation to laboratory measures of performance. Animal Behaviour 71:1389-1399.

Furuta, S. 1996. Predation on juvenile Japanese flounder (*Paralichthys olivaceus*) by diurnal piscivorous fish: field observations and laboratory experiments. Pages 285-294 *in* Y. Watanabe, Y. Yamashita, and Y. Oozeki, editors. Survival Strategies in Early Life Stages of Marine Resources. Balkema, Rotterdam.

Gazdewich, K.J., and D.P. Chivers. 2002. Acquired predator recognition by fathead minnows: influence of habitat characteristics on survival. Journal of Chemical Ecology 28:439-445.

Giles, N. 1984. Development of the overhead fright response in wild and predator naïve three-spined sticklebacks, *Gasterosteus aculeatus* L. Animal Behaviour 32:276-279.

Gillen, A.L., R.A. Stein, and R.F. Carline. 1981. Predation by pellet reared tiger muskellunge on minnows and bluegills in experimental systems. Transactions of the American Fisheries Society 110:197-209.

Ginetz, R.M., and P.A. Larkin. 1976. Factors affecting rainbow trout (*Salmo gairdneri*) predation on migrant fry of sockeye salmon (*Oncorhynchus nerka*). Journal of the Fisheries Research Board of Canada 33(1):19-24.

Goolish, E.M. 1989. The scaling of aerobic and anaerobic muscle power in the rainbow trout (*Salmo gairdneri*). The Journal of Experimental Biology 147:493-505.

Grant, J.W.A., and D.L.G. Noakes. 1987. Escape behavior and use of cover by young-of-the-year brook trout, *Salvelinus fontinalis*. Canadian Journal of Fisheries and Aquatic Sciences 44:1390-1396.

Greene, D.M., Jr. 1964. A comparison of stamina of brook trout from wild and domesticated parents. Transactions of the American Fisheries Society 93:96-100.

Gregory, T.R., and C.M. Wood. 1998. Individual variation and interrelationships between swimming performance, growth rate, and feeding in juvenile rainbow

trout (*Oncorhynchus mykiss*). Canadian Journal of Fisheries and Aquatic Sciences 55:1583-1590.

Grimes, C.B. 1998. Marine stock enhancement: sound management or techno-arrogance? Fisheries 23:18-24.

Heath, M.R. 1993. The role of escape reactions in determining the size distribution of prey captured by herring larvae. Environmental Biology of Fishes 38:331-344.

Heck, K.L., and T.A. Thoman. 1981. Experiments on predator-prey interactions in vegetated aquatic habitats. Journal of Experimental Marine Biology and Ecology 53:125-134.

Helfman, G.S. 1989. Threat-sensitive predator avoidance in damselfish-trumpetfish interactions. Behavioral Ecology and Sociobiology 24:47-58.

Hernández, L.P. 2000. Intraspecific scaling of feeding mechanics in an ontogenetic series of zebrafish, *Danio rerio*. The Journal of Experimental Biology 203:3033-3043.

Hilborn, R., and J. Winton. 1993. Learning to enhance salmon production: lessons from the Salmonid Enhancement Program. Canadian Journal of Fisheries and Aquatic Sciences 50:2043-2056.

Hill, M.S., G.B. Zydlewski, and W.L. Gale. 2006. Comparisons between hatchery and wild steelhead trout (*Oncorhnychus mykiss*) smolts: physiology and habitat use. Canadian Journal of Fisheries and Aquatic Sciences 63:1627-1638.

Holt, G.J. 1993. Feeding larval red drum on microparticulate diets in a closed

recirculating water system. Journal of the World Aquaculture Society 24(2):225-230.

Holt, G.J., and S.A. Holt. 2000. Vertical distribution and the role of physical processes in the feeding dynamics of two larval sciaenids *Sciaenops ocellatus* and *Cynoscion nebulosus*. Marine Ecology Progress Series 193:191-190.

Hossain, M.A.R., M. Tanaka, and R. Masuda. 2002. Predator-prey interaction between hatchery-reared Japanese flounder juvenile, *Paralichthys olivaceus*, and sandy shore crab, *Matuta lunaris*: daily rhythms, anti-predator conditioning and starvation. Journal of Experimental Marine Biology and Ecology 267:1-14.

Houde, E.D. 1987. Fish early life dynamics and recruitment variability. American Fisheries Society Symposium 2:17-29.

Howell, B.R., and S.M. Baynes. 1993. Are hatchery-reared sole equipped for survival in the sea? ICES Council Meeting Papers, ICES, Copenhagen, Denmark.

Hoxmeier, R.J.H., D.H. Wahl, M.L. Hooe, and C.L. Pierce. 2004. Growth and survival of larval walleyes in response to prey availability. Transactions of the American Fisheries Society 133:45-54.

Hunter, J.R. 1972. Swimming and feeding behavior of larval anchovy *Engraulis mordax*. Fishery Bulletin 70(3):821-838.

Hunter, S.A., M.S. Bay, M.L. Martin, and J.S. Hatfield. 2002. Behavioral effects of environmental enrichment on harbor seals (*Phoca vitulina concolor*) and gray seals (*Halichoerus grypus*). Zoo Biology 21:375-387.

Huntingford, F.A. 1984. Some ethical issues raised by studies of predation and aggression. Animal Behaviour 32:210-215.

Huskey, S.H. 2003. Functional and morphological bases of intraspecific variation in the feeding ecomorphology of largemouth bass, *Micropterus salmoides*. Doctoral dissertation. Florida Institute of Technology, Melbourne.

Hyslop, E.J. 1980. Stomach contents analysis – a review of methods and their application. Journal of Fish Biology 17:411-429.

Jarvi, T., and I. Uglem. 1993. Predator training improves the anti-predator behaviour of hatchery reared Atlantic salmon (*Salmo salar*) smolt. Nordic Journal of Freshwater Research 68:63-71.

Jenkins, W.E., M.R. Denson, C.B. Bridgham, M.R. Collins, and T.I.J. Smith. 2004. Year-class component, growth, and movement of juvenile red drum stocked seasonally in a South Carolina Estuary. North American Journal of Fisheries Management 24:636-647.

Johnsen, B.O., and O. Ugedal. 1986. Feeding by hatchery-reared and wild brown trout, *Salmo trutta* L., in a Norwegian stream. Aquaculture and Fisheries Management 17:281-287.

Johnsen, B.O., and O. Ugedal. 1989. Feeding by hatchery-reared brown trout, *Salmo trutta* L. released in lakes. Aquaculture and Fisheries Management 20:97-104.

Kats, L.B., and L.M. Dill. 1998. The scent of death: chemosensory assessment of predation risk by prey animals. Ecoscience 5:361-394.

Kelley, J.L., and A.E. Magurran. 2003. Learned predator recognition and antipredator responses in fishes. Fish and Fisheries 4:216-226.

Kellison, G.T., D.B. Eggleston, and J.S. Burke. 2000. Comparative behaviour of survival of hatchery-reared versus wild summer flounder (*Paralichthys dentatus*). Canadian Journal of Fisheries and Aquatic Sciences 57:1870-1877.

Kempermann, G., D. Gast, and F.H. Gage. 2002. Neuroplasticity in old age: sustained fivefold induction of hippocampal neurogenesis by long-term environmental enrichment. Annals of Neurology 52:135-143.

Kerfoot, K.C., D.L. Kellogg, and J.R. Strickler, Jr. 1980. Visual observations of live zooplankters: evasion, escape and chemical defenses. Pages 10-27 *in* W.C. Kerfoot, editor. Evolution and Ecology of Zooplankton Communities. The University Press of New England, New Hampshire.

Kitada, S. 1999. Effectiveness of Japan's stock enhancement programmes: current perspectives. Pages 103-131 *in* B.R. Howell, E. Moks-ness, and T. Svåsand, editors. Stock Enhancement and Sea Ranching. Fishing News Books, Oxford, England.

Kolok, A.S., E.P. Plaisance, and A. Abdelghani. 1998. Individual variation in the swimming performance of fishes: an overlooked source of variation in toxicity studies. Environmental Toxicology and Chemistry 17(2):282-285.

Koumoundouros, G., D.G. Sfakianakis, P. Divanach, and M. Kentouri. 2002. Effect of temperature on swimming performance of sea bass juveniles. Journal of Fish Biology 60:923-932.

Krebs, J.M., and R.G. Turingan. 2003. Intraspecific variation in gape-prey size

relationships and feeding success during early ontogeny in red drum, *Sciaenops ocellatus*. Environmental Biology of Fishes 66:75-84.

Kristensen, E.A., and G.P. Closs. 2004. Anti-predator response of naïve and experienced common bully to chemical alarm cues. Journal of Fish Biology 64:643-652.

Kristiansen, T.S., H. Ottera, and T. Svasand. 2000. Size-dependent mortality of juvenile Atlantic cod, estimated from recaptures of released cod and tagged wild cod. Journal of Fish Biology 56:687-712.

Kucska, B., L. Pál, T. Müller, M. Bòdis, A. Bartos, L. Wágner, F. Husvéth, and M. Bercsényi. 2006. Changing fat content and fatty acid profile of reared pike (*Esox lucius*) fed two different diets. Aquaculture Research 37:96-101.

Langley, C.M. 1996. Search images: selective attention to specific visual features of prey. Journal of Experimental Psychology 22(2):152-163.

Lawrence, E.S., and J.A. Allen. 1983. On the term 'search image'. Oikos 40:313-314.

Lehtiniemi, M. 2005. Swim or hide: predator cues cause species specific reactions in young fish larvae. Journal of Fish Biology 66:1285-1299.

Lorenzen, K. 2005. Population dynamics and potential of fisheries stock enhancement: practical theory for assessment and policy analysis. Philosophical Transactions of the Royal Society B 360:171-189.

MacCall, A.D. 1989. Against marine fish hatcheries: ironies of fishery politics in the technological era. California Cooperative Oceanic Fisheries Investigations

(CalCOFI) Report 30:46-48.

MacKenzie, B.R., and T. Kiørboe. 1995. Encounter rates and swimming behavior of pause-travel and cruise larval fish predators in calm and turbulent laboratory environments. Limnology and Oceanography 40:1278-1289.

MacKenzie, B.R., and T. Kiørboe. 2000. Larval fish feeding and turbulence: a case for the downside. Limnology and Oceanography 45(1):1-10.

Magurran, A.E. 1989. Acquired predator recognition of predator odour in the European minnow (*Phoxinus phoxinus*). Ethology 82:216-233.

Magurran, A.E. 1990. The inheritance and development of minnow anti-predator behaviour. Animal Behaviour 39:834-842.

Magurran, A.E., and B.H. Seghers. 1990. Population differences in predator recognition and attack cone avoidance in the guppy (*Poecilia reticulata*). Animal Behavior 40:443-452.

Malavasi, S., V. Georgalas, M. Lugli, P. Torricelli, and D. Mainardi. 2004. Differences in the pattern of antipredator behaviour between hatchery-reared and wild European sea bass juveniles. Journal of Fish Biology 65(Supplement A):143-155.

Manatunge, J., T. Asaeda, and T. Priyadarshana. 2000. The influence of structural complexity on fish-zooplankton interactions: a study using artificial submerged macrophytes. Environmental Biology of Fishes 58:425-438.

Martínez, M, H. Guderley, J.-D. Dutil, P.D. Winger, P. He, and S.J. Walsh. 2003.

Condition, prolonged swimming performance and muscle metabolic capacities of cod *Gadus morhua*. The Journal of Experimental Biology 206:503-511.

Maynard, D.J., G.C. McDowell, E.P. Tezak, and T.A. Flagg. 1996. Effects of diets supplemented with live food on the foraging behavior of cultured fall chinook salmon. The Progressive Fish Culturist 58:187-191.

McCormick, M.I., and T.H. Holmes. 2006. Prey experience of predation influences mortality rates at settlement in a coral reef fish, *Pomacentrus amboinensis*. Journal of Fish Biology 68:969-974.

McDonald, D.G., C.L. Milligan, W.J. McFarlane, S. Croke, S. Currie, B. Hooke, R.B. Angus, B.L. Tufts, and K. Davidson. 1998. Condition and performance of juvenile Atlantic salmon (*Salmo salar*): effects of rearing practices on hatchery fish and comparison with wild fish. Canadian Journal of Fisheries and Aquatic Sciences 55:1208-1219.

McEachron, L.W., C.E. McCarty, and R.R. Vega. 1995. Beneficial uses of marine fish hatcheries: enhancement of red drum in Texas coastal waters. American Fisheries Society Symposium 15:161-166.

McEachron, L.W., R.L. Colura, B.W. Bumguardner, and R. Ward. 1998. Survival of stocked red drum in Texas. Bulletin of Marine Science 62(2):359-368.

McNeil, W.J. 1991. Expansion of cultured Pacific salmon into marine ecosystems. Aquaculture 98:173-183.

Minello, T.J., and R.J. Zimmerman. 1983. Fish predation on juvenile brown shrimp, *Penaeus aztecus* Ives: the effect of simulated *Spartina* structure on predation

rates. Journal of Experimental Marine Biology and Ecology 72:211-231.

Mirza, R.S., and D.P. Chivers. 2001. Chemical alarm signals enhance survival of brook charr (*Salvelinus fontinalis*) during encounters with predatory chain pickerel (*Esox niger*). Ethology 107:989-1005.

Moring, J.R. 1986. Stocking anadromous species to restore or enhance fisheries. Pages 59-74 *in* R.H. Stroud, editor. Fish Culture in Fisheries Management. American Fisheries Society, Bethesda, Maryland.

Munakata, A., B. Th. Björnsson, E. Jönsson, M. Amano, K. Ikuta, S. Kitamura, T. Kurokawa§, and K. Aida. 2000. Post-release adaptation processes of hatchery-reared honmasu salmon parr. Journal of Fish Biology 56:163-172.

Munro, J.L., and J.D. Bell. 1997. Enhancement of marine fisheries resources. Reviews in Fisheries Science 5(2):185-222.

Nelson, J.A. 1989. Critical swimming speeds of yellow perch *Perca flavescens*: comparison of populations from a naturally acidic lake and a circumneutral lake in acid and neutral water. The Journal of Experimental Biology 145:239-245.

Nelson, J.A., P.A. Gotwalt, and J.W. Snodgrass. 2003. Swimming performance of blacknose dace (*Rhinichthys atratulus*) mirrors home-stream current velocity. Canadian Journal of Fisheries and Aquatic Sciences 60:301-308.

Nicoletto, P.F., and A. Kodric-Brown. 1999. The relationship among swimming performance, courtship behavior, and carotenoid pigmentation of guppies in four rivers in Trinidad. Environmental Biology of Fishes 55:227-235.

Nødtvedt, M., A. Fernö, J. Gjøsæter, and P. Steingrund. 1999. Anti-predator behaviour of hatchery-reared and wild juvenile Atlantic cod (*Gadus morhua* L.), and the effect of predator training. Pages 350-362 *in* B.R. Howell, E. Moksness and T. Svåsand, editors. Stock Enhancement and Sea-ranching. Blackwell Science, Ltd., Oxford, United Kingdom.

Nordeide, J.T., and A.G.V. Salvanes. 1991. Observations on reared newly released and wild cod (*Gadus morhua* L.) and their potential predators. ICES Marine Science Symposium 136-146.

O'Grady, M.F. 1983. Observations on the dietary habits of wild and stocked brown trout, *Salmo trutta* L., in Irish lakes. Journal of Fish Biology 22:593-601.

Ojanguren, A.F., and F. Braña. 2003. Effects of size and morphology on swimming performance in juvenile brown trout (*Salmo trutta* L.). Ecology of Freshwater Fish 12:241-246.

Olla, B.L., and M.W. Davis. 1989. The role of learning and stress in predator avoidance of hatchery-reared coho salmon (*Oncorhynchus kisutch*) juveniles. Aquaculture 76:209-214.

Olla, B.L., M.W. Davis, and C.H. Ryer. 1992. Foraging and predator avoidance in hatchery-reared Pacific salmon: achievement of behavioral potential. Pages 5-12 *in* J.E. Thorpe and F.A. Huntingford, editors. World Aquaculture Workshops, Number 2: The Importance of Feeding Behavior for the Efficient Culture of Salmonid Fishes. World Aquaculture Society, Baton Rouge, Louisiana.

Olla, B.L., M.W. Davis, and C.H. Ryer. 1994. Behavioural deficits in hatchery-reared fish: potential effects on survival following release. Aquaculture and Fisheries

Management 25(Supplement 1):19-34.

Olla, B.L., M.W. Davis, and C.H. Ryer. 1998. Understanding how the hatchery environment represses or promotes the development of behavioral survival skills. Bulletin of Marine Science 62(2):531-550.

Osse, J.W.M., and J.G.M. van den Boogaart. 1999. Dynamic morphology of fish larvae, structural implications of friction forces in swimming, feeding and ventilation. Journal of Fish Biology 55(Supplement A):156-174.

Paglianti, A., and P. Domenici. 2006. The effect of size on the timing of visually mediated escape behavior in staghorn sculpin *Leptocottus armatus*. Journal of Fish Biology 68:1177-1191.

Paszkowski, C., and B.L. Olla. 1985. Foraging behaviour of hatchery produced coho salmon (*Oncorhynchus kisutch*) smolts on live prey. Canadian Journal of Fisheries and Aquatic Sciences 42:1915-1921.

Patten, B.G. 1977. Body size and learned avoidance as factors affecting predation on coho salmon, *Oncorhynchus kisutch*, fry by torrent sculpin, *Cottus rhotheus*. Fisheries Bulletin 75(2):457-459.

Pattillo, M.E., T.E. Czapla, D.M. Nelson, and M.E. Monaco. 1997. Distribution and abundance of fishes and invertebrates in Gulf of Mexico estuaries. Volume II: Species life history summaries. ELMR Report No. 11. NOAA/NOS Strategic Environmental Assessments Division, Silver Spring, Maryland. 377 pages.

Peters, K.M., and R.H. McMichael, Jr. 1987. Early life history of the red drum *Sciaenops ocellatus* (Pisces: Sciaenidae) in Tampa Bay, Florida. Estuaries

10(2):92-107.

Piggins, D.J., and C.P.R. Mills. 1985. Comparative aspects of the biology of naturally produced and hatchery-reared Atlantic salmon smolts (*Salmo salar* L.). Aquaculture 45:321-333.

Pitcher, T.J., and J.K. Parrish. 1993. Functions of shoaling behaviour in teleosts. Pages 364-439 *in* T.J. Pitcher, editor. The Behaviour of Teleost Fishes. 2nd edition. Chapman and Hall, London, United Kingdom.

Poling, K.R., and L.A. Fuiman. 1999. Behavioral specialization in developing sciaenids and its relationship to morphology and habitat. Environmental Biology of Fishes 54:119-133.

Pon, L.B., S.G. Hinch, G.N. Wagner, A.G. Lotto, and S.J. Cooke. 2007. Swimming performance and morphology of juvenile sockeye salmon, *Oncorhynchus nerka*: comparison of inlet and outlet fry populations. Environmental Biology of Fishes 78:257-269.

Reidy, S.P., S.R. Kerr, and J.A. Nelson. 2000. Aerobic and anaerobic swimming performance of individual Atlantic cod. The Journal of Experimental Biology 203:347-357.

Reirez, L., A.G. Nicieza, F. Braña. 1998. Prey selection by experienced and naïve juvenile Atlantic salmon. Journal of Fish Biology 53:100-114.

Richard, B.A., and P.C. Wainwright. 1995. Scaling the feeding mechanism of largemouth bass (*Micropterus salmoides*): kinematics of prey capture. The Journal of Experimental Biology 198:419-433.

Richards, W.J., and R.E. Edwards. 1986. Stocking to restore or enhance marine fisheries. Pages 75-80 *in* R.H. Stroud, editor. Fish Culture in Fisheries Management. American Fisheries Society, Bethesda, Maryland.

Rooker, J.R., G.J. Holt, and S.A. Holt. 1998. Vulnerability of newly settled red drum (*Sciaenops ocellatus*) to predatory fish: is early life survival enhanced by seagrass meadows? Marine Biology 131:145-151.

Rooker, J.R., S. Holt, G.J. Holt, and L.A. Fuiman. 1999. Spatial and temporal variability in growth, mortality, and recruitment potential of postsettlement red drum, *Sciaenops ocellatus*, in a subtropical estuary. Fishery Bulletin 97(3):581-590.

Ryer, C.H., and B.L. Olla. 1998. Shifting the balance between foraging and predator avoidance: the importance of food distribution for a schooling pelagic forager. Environmental Biology of Fishes 52:467-475.

Salvanes, A.G.V., and V.A. Braithwaite. 2005. Exposure to variable spatial information in the early rearing environment generates asymmetries in social interactions in cod (*Gadus morhua*). Behavioral Ecology and Sociobiology 59:250-257.

Savino, J.F., and R.A. Stein. 1982. Predator-prey interaction between largemouth bass and bluegills as influenced by simulated, submersed vegetation. Transactions of the American Fisheries Society 111:255-266.

Scharf, F.S. 2000. Patterns in abundance, growth, and mortality of juvenile red drum across estuaries on the Texas coast with implications for recruitment and stock enhancement. Transactions of the American Fisheries Society 129:1207-1222.

Seghers, B.H. 1974. Schooling behavior in the guppy (*Poecilia reticulata*): an evolutionary response to predation. Evolution 28(3):486-489.

Serafy, J.E., J.S. Ault, T.R. Capo, and D.R. Schultz. 1999. Red drum, *Sciaenops ocellatus* L., stock enhancement in Biscayne Bay, FL, USA: assessment of releasing unmarked early juveniles. Aquaculture Research 30:737-750.

Shively, R.S., T.P. Poe, M.B. Sheer, and R. Peters. 1996. Criteria for reducing predation by northern squawfish near juvenile salmonid bypass outfalls at Columbia River dams. Regulated Rivers: Research and Management 12:493-500.

Smith, M.E., and L.A. Fuiman. 2004. Behavioral performance of wild-caught and laboratory-reared red drum *Sciaenops ocellatus* (Linnaeus) larvae. Journal of Experimental Marine Biology and Ecology 302:17-33.

Smith, T.I.J., W.E. Jenkins, M.R. Denson, and M.R. Collins. 2001. Stock enhancement research with anadromous and marine fishes in South Carolina. Pages 175-189 *in* Y. Nakamura, J.P. McVey, K. Leber, C. Neidig, S. Fox, and K. Churchill, editors. Ecology of Aquaculture Species and Enhancement of Stocks. Proceedings of the Thirtieth U.S. – Japan Meeting on Aquaculture. UJNR Technical Report No. 30. Mote Marine Laboratory, Sarasota, Florida.

Sogard, S.M., and B.L. Olla. 1993. The influence of predator presence on utilization of artificial seagrass habitats by juvenile walleye pollock, *Theragra chalcogramma*. Environmental Biology of Fishes 37:57-65.

Sosiak, A.J., R.G. Randall, and J.A. MacKenzie. 1979. Feeding by hatchery-reared and wild Atlantic salmon (*Salmo salar*) parr in streams. Journal of the Fisheries

Research Board of Canada 36:1408-1412.

Soto, M.A., G.J. Holt, and J.R. Rooker. 1998. Food habits and dietary overlap of newly settled red drum (*Sciaenops ocellatus*) and Atlantic croaker (*Micropogonias undulatus*) from Texas seagrass meadows. Gulf Research Reports 10:41-55.

Steingrund, P., and A. Fernö. 1997. Feeding behaviour of reared and wild cod and the effect of learning: two strategies of feeding on the two-spotted goby. Journal of Fish Biology 51:334-348.

Stunz, G.W., and T.J. Minello. 2001. Habitat-related predation on juvenile wild-caught and hatchery-reared red drum *Sciaenops ocellatus* (Linnaeus). Journal of Experimental Marine Biology and Ecology 260:13-25.

Stunz, G.W., P.S. Levin, and T.J. Minello. 2001. Selection of estuarine nursery habitats by wild-caught and hatchery-reared juvenile red drum in laboratory mesocosms. Environmental Biology of Fishes 61:305-313.

Stunz, G.W., T.J. Minello, and P.S. Levin. 2002. Growth of newly settled red drum, *Sciaenops ocellatus* in different estuarine habitat types. Marine Ecology Progress Series 238:227-236.

Suboski, M.D., and J.J. Templeton. 1989. Life skills training for hatchery fish: social learning and survival. Fisheries Research 7:343-53.

Sundström, L.F., and J.I. Johnsson. 2001. Experience and social environment influence the ability of young brown trout to forage on live novel prey. Animal Behaviour 61:249-255.

Svasand, T., T.S. Kristiansen, T. Pederson, A.G.V. Salvanes, R. Engelsen, G. Naevdal, and M. Nodtvedt. 2000. The enhancement of cod stocks. Fish and Fisheries 1:173-205.

Tátrai, I., and A. Herzig. 1995. Effect of habitat structure on the feeding efficiency of young stages of razor fish (*Pelecus cultratus* (L.)): an experimental approach. Hydrobiologia 299:75-81.

Taylor, E.B., and J.D. McPhail. 1985. Variation in burst swimming and prolonged swimming performance among British Columbia population of coho salmon, *Oncorhynchus kisutch*. Canadian Journal of Fisheries and Aquatic Sciences 42:2029-2033.

Thorstad, E.B., B. Finstad, F. Økland, R.S. McKinley, and R.K. Booth. 1997. Endurance of farmed and sea-ranched Atlantic salmon *Salmo salar* L. at spawning. Aquaculture Research 28:635-640.

Vega R.R., C. Chavez, C.J. Stolte, and D. Abrego. 2003. Marine fish distribution report, 1991-1999. Management Data Series No. 212, Texas Parks and Wildlife Department. Coastal Fisheries Division, Austin Texas, 70 pages.

Vilhunen, S. 2006. Repeated antipredator conditioning: a pathway to habituation or to better avoidance? Journal of Fish Biology 68:25-43.

Vincent, R.E. 1960. Some influences of domestication upon three stocks of brook trout (*Salvelinus fontinalis* Mitchill). Transactions of the American Fisheries Society 89:35-52.

Walker, J.A. 1997. QuickSAND. Quick Smoothing and Numerical Differentiation for

the power MacIntosh. http://www.usm.maine.edu/~walker/software.html

Walker, J. A. 1998. Estimating velocities and accelerations of animal locomotion: a simulation experiment comparing numerical differentiation algorithms. The Journal of Experimental Biology 201:981-995.

Walker, J.A., C.K. Ghalambor, O.L. Griset, D. McKenney, and D.N. Reznick. 2005. Do faster starts increase the probability of evading predators? Functional Ecology 19:808-815.

Ware, D.M. 1971. Predation by rainbow trout (*Salmo gairdneri*): the effect of experience. Journal of the Fisheries Research Board of Canada. 28:1847-1852.

Webb, P.W. 1976. The effect of size on the fast-start performance of rainbow trout *Salmo gairdneri*, and a consideration of piscivorous predator-prey interactions. The Journal of Experimental Biology 65:157-177.

Webb, P.W., and D. Weihs. 1984. Optimal avoidance and evasion tactics in predator-prey interactions. Journal of Theoretical Biology 106:189-206.

Webb, P.W., and D. Weihs. 1986. Functional locomotor morphology of early life stages of fishes. Transactions of the American Fisheries Society 115:115-127.

Weber, E.D., and K.D. Fausch. 2003. Interactions between hatchery and wild salmonids in streams: differences in biology and evidence for competition. Canadian Journal of Fisheries and Aquatic Sciences 60:1018-1036.

Welcomme, R.L., and D.M. Bartley. 1998. Current approaches to the enhancement of fisheries. Fisheries Management and Ecology 5(5):351-382.

Westerman, M.E., and G.J. Holt. 1994. RNA:DNA ratio during the critical period and early larval growth of the red drum *Sciaenops ocellatus*. Marine Biology 121:1-9.

Wiley, R.W., R.A. Whaley, J.B. Satake, and M. Fowden. 1993. An evaluation of the potential for training trout in hatcheries to increase post-stocking survival in streams. North American Journal of Fisheries Management 13:171-177.

Winfield, I.J. 1986. The influence of simulated aquatic macrophytes on the zooplankton consumption rate of juvenile roach, *Rutilus rutilus*, rudd, *Scardinius erythrophthalmus*, and perch, *Perca fluviatilis*. Journal of Fish Biology 29(Supplement A):37-48.

Wintzer, A.P., and P.J. Motta. 2005. A comparison of prey capture kinematics in hatchery and wild *Micropterus salmoides floridanus*: effects of ontogeny and experience. Journal of Fish Biology 67:409-427.

Wisenden, B.D., K.A. Vollbrecht, and J.L. Brown. 2004. Is there a fish alarm cue? Affirming evidence from a wild study. Animal Behaviour 67:59-67.

Woodward, A.G. 2000. Red drum stock enhancement in Georgia: a responsible approach. Coastal Resources Division, Georgia Department of Natural Resources, Brunswick, Georgia. 12 pages.

Ydenberg, R.C., and L.M. Dill. 1986. The economics of fleeing from predators. Advances in the Study of Behavior 16:229-249.

VITA

Jessica Louise Beck graduated from the Indiana University of Pennsylvania in May 1998 with a Bachelor of Science degree in biology. In August 2002, she received a Master of Science in marine biology from the Biological Sciences Department at the Florida Institute of Technology. In August 2002, she entered the Doctoral Program in the Department of Wildlife and Fisheries Sciences at Texas A&M University, and received her Ph.D. in May of 2008.

Permanent address: c/o Dr. Jay Rooker, 5007 Avenue U, Galveston, Texas, 77551